

# **INVERTEBRATE PRODUCTION WITHIN VARIOUS HABITATS OF A BRAIDED RIVER**

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## ABSTRACT

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Seepage streams within "flood overflow" channels are important microhabitats within braided rivers. They are important foraging zones for wading birds and may contribute to the ability of the invertebrate community to recover from disturbance. Production of dominant invertebrates was estimated along a three kilometre study reach of the Rakaia River for various channel types ranging from seepage stream microhabitats within secondary channels to the largest braids in the central river bed. The seepage and spring stream microhabitats received varying exposure to elevated summer flows, freshes, and were inundated by flows of greater than approximately 200 cumecs. Four quadrats were randomly located within 10 metre sampling transects in riffles of seepage and spring stream microhabitat in addition to minor and major braids. Riffles were sampled at six week intervals from October 1997 to August 1998, with no riffle sampled more than once. Production was estimated using the size frequency method. Seepage stream microhabitats were the most productive sites examined. Production was estimated to be 10.3 g DW m<sup>-2</sup> yr<sup>-1</sup> for a perennial seepage stream, 3.2 g DW m<sup>-2</sup> yr<sup>-1</sup> for a baseflow seepage stream, 1.0 g DW m<sup>-2</sup> yr<sup>-1</sup> for a baseflow spring stream, and 0.5 g DW m<sup>-2</sup> yr<sup>-1</sup> and 0.6 g DW m<sup>-2</sup> yr<sup>-1</sup> respectively for the minor and major braids. The two types of seepage stream had significantly greater production than the minor and major braids. Invertebrate production is likely to be affected by gradients of disturbance, temperature, algal abundance, and organic matter retention. Frequent and

unpredictable flooding probably restricts production in the minor and major braids but helps maintain structure of seepage and spring stream microhabitat in secondary "flood overflow" channels.

## CHAPTER 1

# GENERAL INTRODUCTION

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### Braided river habitats

Braided rivers in the South Island of New Zealand contain an exceptionally diverse range of habitats because of their inherent instability and unique morphology. They have continually changed course, and wetland areas, such as swamps and marshes, have developed alongside them (Stout, 1998). Considerable variation in relief across braided rivers has provided a variety of terrestrial and aquatic habitats of varying age. Within the braids and small side channels, the main types of habitat are riffles, pools, and runs. Riffles are considered to be particularly important as they are sites of relatively high invertebrate production, wading bird feeding activity (Sagar, 1983a; Pierce, 1979; 1983), and provide important habitat for native and salmonid fish (Davis *et al.*, 1983). Perhaps the smallest but most productive habitats within the riverbeds are seepage and spring streams that lie within the gravel expanses between the braids. They contain relatively high numbers of invertebrate species, provide habitat for native fish, and are frequented by the various birds that utilise braided river habitats.

## Seepage microhabitat as foraging zones for wading birds.

Six endemic bird species utilise the South Island's braided rivers as habitat (Maloney *et al.*, 1997). They are of particular conservation interest and include the wrybilled plover (*Anarhynchus frontalis*), banded dotterel (*Charadrius bicinctus*), pied stilt (*Himantopus himantopus leucocephalus*), black stilt (*Himantopus novaezelandiae*), black - billed gull (*Larus bulleri*), and black - fronted tern (*Sterna albobriata*). The black stilt is considered "endangered" with fewer than 100 individuals remaining, while both the endemic wrybill, and the black fronted tern are regarded as "threatened" because of recent declines in their populations (Bell, 1986; Tisdall, 1994 cited in Hughey, 1998). O'Donnell & Moore (1983) estimated that 75% of the wrybill population of Canterbury could be found on the Rakaia River during the breeding season, a significant proportion of their total population. The Rakaia River is also an important breeding ground for the black - fronted tern (O'Donnell & Moore, 1983). River terraces, scarps, and bars, provide major nesting locations for these birds, while aquatic habitats provide their main feeding areas. They preferentially select the topographically highest areas of bare shingle on which to nest, since they are least likely to be flooded (Stead, 1932). However, recent vegetation encroachment is seriously reducing the availability of this habitat (Hughey, 1998). These birds forage in a variety of aquatic habitats, but the shallow channel edges are used most extensively (O'Donnell & Moore, 1989; Hughey, 1989). Both the wrybill and black - fronted tern feed heavily on the mayfly *Deleatidium*.

Hughey (1997) studied the diet of the wrybill on the Ashley and Rakaia Rivers during the breeding season. While invertebrate prey of both terrestrial and aquatic origin was consumed, *Deleatidium* larvae comprised 30% of the wrybill diet in the Rakaia River, and about 20% in the Ashley River. Caddisfly larvae were not present in the diet of wrybills on the Rakaia River, but comprised up to 70% of the diet on the Ashley River. Pierce (1979) attributed switches between riparian and aquatic prey to foraging "profitability". He considered riparian foraging to be more "profitable" after periods of flooding. Hence birds from the more flood-prone and larger Rakaia River had a lower proportion of aquatic invertebrates in their diet.

Hughey *et al.* (1989) also compared the biomass and composition of benthic macroinvertebrate assemblages between channel types on two braided rivers. Primarily they were concerned with the effect of the differing hydrologic regimes on the food supply of endemic and native bird species. Braids and seepage channels of the Waimakariri and the Ashley Rivers were sampled monthly between September 1985 and August 1986. On the Waimakariri River, major braids were those visually estimated to have a discharge greater than  $5 \text{ m}^3\text{s}^{-1}$  and on the smaller Ashley River those greater than  $1 \text{ m}^3\text{s}^{-1}$ . Minor braids had correspondingly lower discharges. Hughey *et al.* (1989) found that seepage channels had the highest densities, biomass, and diversity of invertebrates. Hughey (1998) also found that the home ranges of wrybills were smallest where

the greatest proportion of minor braids and seepage channels occurred. He attributed this relationship to the greater food availability they provided.

### **Habitats utilised by fish**

The fish fauna of Canterbury's braided rivers is made up of 18 to 20 species (Davis *et al*, 1983), six of which are typically present in their lower reaches for most of the year. This latter group includes the torrent fish (*Cheimarrichthys fosteri*), blue - gilled bully (*Gobiomorphus hubbsi*), upland bully (*Gobiomorphus breviceps*), long - finned eel (*Anguilla dieffenbachii*), quinnat salmon (*Oncorhynchus tshawytscha*) and brown trout (*Salmo trutta*) (Davis *et al.*, 1983). Activities undertaken by fish in the rivers are variable in space and time, and include spawning, incubation, hatching, feeding, resting, and migration. In the larger rivers, the dominant habitats are moderately deep and relatively fast flowing pools with little cover, extensive moderately uniform runs, and broad, shallow riffles with considerable areas of white water (Davis *et al*, 1983). Where, and when they occur, debris clusters form ideal habitat for several species. The native fish fauna occur predominantly in riffles of the various braids and small side channels. These riffles have been described as the main food producing areas of braided Canterbury rivers (Davis *et al.*, 1983), particularly in the alpine rivers typically discoloured with glacial flour. Glova & Duncan (1985) described the run and pool areas of the Rakaia River as relatively unproductive areas of silted gravels and cobbles. Pools of the main channels of the Rakaia River also appear to be of little



importance for salmonid and native fish, because they lack cover and offer limited feeding opportunities (Davis *et al.*, 1983).

One of the most common, native fish species is the torrent fish (Glova *et al.*, 1985). Its typical habitat is the downstream ends of riffles and rapids, where they show a preference for swift, broken, but shallow water, most often between 200 and 300 mm deep (Davis *et al.*, 1983). They also prefer moderately small substrates (< 50 mm: Jowett & Richardson, 1996) and are less prevalent where the substrate becomes armoured and consolidated by deposited silt and sand (McDowall, 1990). The habitat of blue - gilled bullies is very similar and the two species are often found together (Davis *et al.*, 1983). Juvenile long and short - finned eels are the most versatile of the more common native species, being found in habitats varying from still to broken water, and clean gravel to silted substrate. Larger eels prefer sizeable instream cover such as debris clusters, and overhanging banks. Upland bullies, occur in widely ranging habitats, but prefer low velocity water less than 0.1 m deep (Jowett & Richardson, 1995). Mosley (1983) suggested the cooler temperatures of seepage and spring flow provided a thermal refugia to the various fish species during brief periods of high water temperature during summer.

### Seepage microhabitats - refugia and colonisation epicentres?

Scrimgeour *et al.* (1988) suggested that disconnected pools, and minor braids provide an important source of aquatic macroinvertebrates from which recolonisation of major braids could proceed following severe flooding. In the Ashley River, recovery of aquatic invertebrates following a large flood was essentially complete after 132 days. Scrimgeour *et al.* (1988) noted that the gradual increases in the abundance of Deleatidium larvae could not be explained solely by oviposition or hatching of eggs present in the substratum since many larvae were too large. They therefore concluded that colonisation from refuge areas such as river margins, and minor braids was likely to be important. During their study they also observed larval Aoteapsyche, Hydrobiosis, and Psilochorema colonising a minor braid from a formerly disconnected upstream pool during a small fresh 44 days after the flood. This led them to suggest that pools created during high flows receive invertebrates during spates, and when reconnected to the main channel act as important sources of colonists.

Drift between minor ( $<1 \text{ m}^3\text{s}^{-1}$ ), intermediate ( $<10 \text{ m}^3\text{s}^{-1}$ ) and major braids ( $>40 \text{ m}^3\text{s}^{-1}$ ) was studied quantitatively and seasonally in the Rakaia River by Sagar & Glova (1992). They found that Deleatidium comprised more than 85% of the drift in all seasons except autumn when Trichoptera and Chironomidae comprised a larger proportion of the drift. They also found significant differences in drift density between the three channel types

during interflood periods in all seasons except autumn when drift densities were highest but not different between channel types. During winter when discharge was low and least variable, and when benthic invertebrate densities were highest, drift density was greatest in the major channels and lowest in the minor channels (Table 1). However, during spring and summer when the density of the benthos was lowest following a series of large floods, drift density was highest in the minor channels (Table 1). These findings suggest that streams with discharges less than  $1 \text{ m}^3\text{s}^{-1}$ , including seepage streams, may play an important role in maintaining invertebrate densities within the greater riverbed particularly during spring and summer.

Table 1. Mean numbers of drifting invertebrates per  $100 \text{ m}^{-3}$  of water filtered ( $2 \times \text{SE}$ ) (from Sagar & Glova, 1992).

Season	Channel type (discharge)		
	Minor	Intermediate	Major
	(< $1 \text{ m}^3\text{s}^{-1}$ )	(< $10 \text{ m}^3\text{s}^{-1}$ )	(> $40 \text{ m}^3\text{s}^{-1}$ )
Autumn	158.8 (41.2)	136.9 (15.4)	167.3 (35.6)
Winter	74.6 (13.0)	100.1 (18.5)	156.4 (22.2)
Spring	49.1 (10.1)	8.4 (1.4)	39.8 (7.4)
Summer	85.7 (31.7)	12.2 (2.0)	61.9 (21.3)

## Study aims

The principal question addressed in this thesis is whether or not secondary production differs among seepage and spring streams compared to braids in the Rakaia River. Secondary production can be

defined "as the living organic matter, or biomass, that is created or produced by an animal population during an interval of time" (Benke, 1984:289). It can be affected by food quality and quantity, temperature, habitat complexity, and biological interactions (Benke, 1984), and also flow - mediated disturbance. I hypothesised that in a river such as the Rakaia, flow - mediated disturbance is likely to have an important if not dominating role, both directly and indirectly in determining invertebrate production. My second aim was to determine what factors are most important in explaining the variation in production within the river bed. Ecological mechanisms determining variability in production within a braided river have not been established, and they are likely to be affected by management practises that alter the magnitude and frequency of both flooding and low flows. For example, changes in bed width in the Waitaki River can be linked to changes in the flow regime resulting from the installation of dams for hydroelectric power development (Mosley & Thompson, 1998). Another example is that stable discharge rivers tend to lack the pool - riffle structures characteristic of more unstable gravel bed rivers (Jowett & Duncan, 1990). Furthermore, in the Rakaia, channels with discharge of  $< 1 \text{ m}^3\text{s}^{-1}$  are most vulnerable to dewatering from low flow (Glova & Duncan, 1985).

## CHAPTER 2

### THE STUDY AREA

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#### Introduction & physical description

The Rakaia is a relatively unmodified and unpolluted braided river in the South Island of New Zealand. It runs from glacial headwaters at 2000 m a. s. l. for nearly 150 kilometres to the Pacific Ocean, on the east coast of the South Island of New Zealand (Figure 1). The Rakaia has a catchment area of 2910 km<sup>2</sup> (Bowden *et al.*, 1983), 2640 km<sup>2</sup> of which is comprised of foothills and mountainous terrain, bounded to the west by the Main Divide. The river has a short, meandering mid section that flows through a hard rock gorge. Below the gorge, the river has an average gradient of about 4.5 m km<sup>-1</sup> (Bowden *et al.*, 1983), and a width of approximately 2 km, although this increases to 5 km near the coast. Individual braids meander at baseflow, and floods change the pattern of braiding markedly (Rundle, 1985).

Within the river, the numerous braids are separated by bars and terraces of varying age and vegetational development. The bars may be draped with sand and sand dunes. They are sporadically vegetated, mostly by a introduced tree lupin, Lupinus arboreus. Introduced grasses, gorse (Ulex europaeus), and broom (Cytisus scoparius) become increasingly dominant on the older bars and terraces. The most obvious

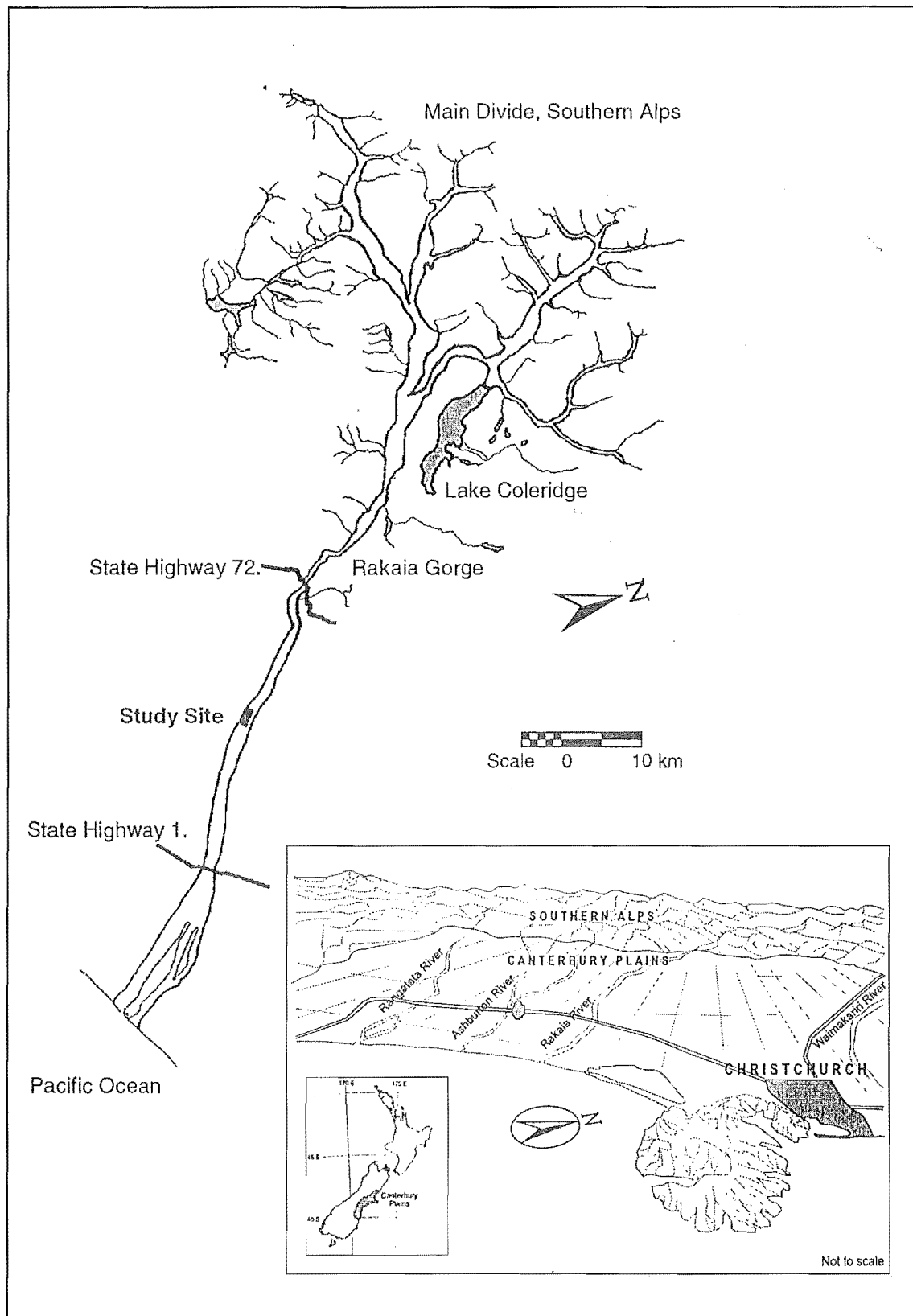


Figure 1. The Rakaia River and its catchment, note study area.

feature of the braided river is the 'active' zone, identified by its lack of vegetation and multiplicity of channels. Any of these channels, but most conspicuously the main channel, can be observed to abruptly shoal and split into a number of smaller channels. Partially vegetated floodplain terraces can occur within or adjacent to the active riverbed and are periodically inundated by overbank flow. Above the gorge, these terraces are most extensive downstream of outcropping tributary fans, debris flows, or bedrock spurs in the river valley. The main morphological characteristics of terraces typically include varied relief, seepage streams, backswamps, and less commonly, sand dunes (Reinfeld & Nanson, 1993). Reinfeld & Nanson (1993) noted that seepage streams occurred in old braid channels, particularly downstream of outcropping tributary fans, and derived much of their discharge from them. Seepage streams are by no means confined to the marginal floodplain terraces along the upper valley, however, and Rundle (1985) noted their occurrence in the 'active' riverbed.

## **Hydrological regime**

The climate of Canterbury is dominated by westerly airflows which carry little moisture east of the Southern Alps. Most flood - producing rainfall is associated with cold fronts preceding low pressure systems originating over the Tasman Sea (Wilson, 1985). Westerly airflows carrying moisture are lifted to traverse the Alps, and in doing so lose their

moisture resulting in high rainfalls on the West Coast and in the headwaters of easterly flowing rivers including the Rakaia. This orographic effect leads to high river flows and may also be accompanied by prolonged periods of high temperature and low humidity on the Canterbury Plains. Rainfall declines with increasing distance to the east of the Main Divide, consequently, about 75% of the rainfall in the Rakaia catchment occurs within 13 km of it. Average annual precipitation in the highest parts of the catchment approach  $8000 \text{ mm yr}^{-1}$ , and declines to about  $1000 \text{ mm yr}^{-1}$  near the western margin of the Canterbury Plains (Bowden *et al.*, 1983). In the upper catchment of the Rakaia, rainfall intensity is commonly over 300 mm in 24 hours (Bowden *et al.*, 1983). Forty one percent of annual rainfall in the highest parts of the catchment occurs from September to December (Bowden *et al.*, 1983). The combination of snowmelt and a predominance of northwesterly airflows during these months is responsible for most of the high flood events recorded at the Rakaia Gorge.

The Rakaia has one of the highest mean flows of the Canterbury rivers. Mean flow at the gorge between 1958 and 1981 was  $200 \text{ m}^3\text{s}^{-1}$ , and the median flow was  $150 \text{ m}^3\text{s}^{-1}$  (Bowden *et al.*, 1983). Formation of ice and snow in the headwaters of the catchment reduce the river's discharge during winter and melting increases it during summer. Flow variability is least in both July, when precipitation is retained as snow and ice, and in February when most of the snow has melted. September typically has the most variable discharge ( $82 \text{ m}^3\text{s}^{-1}$  to  $532 \text{ m}^3\text{s}^{-1}$ ; Bowden



*et al.*, 1983). High discharges occur when temperatures during northwesterly airflows are sufficiently high to release a large volume of melting snow and ice. Conversely, if the temperature in September is low, little snow melt will occur and river discharge will be low (Bowden *et al.*, 1983). Despite seasonal changes in rainfall and discharge, westerly rains can cause floods of greater than  $600 \text{ m}^3\text{s}^{-1}$  at any time of year (Sagar 1986). Floods with a 10 year recurrence interval are estimated to be about  $3800 \text{ m}^3\text{s}^{-1}$  (Griffiths & Glasby, 1985).

Baseflow at the gorge is about  $150 \text{ m}^3\text{s}^{-1}$  after 20 days without rain, and drops to below  $100 \text{ m}^3\text{s}^{-1}$  after 30 to 40 days if snow melt is ignored (Bowden *et al.*, 1983). Between 16 and  $26 \text{ m}^3\text{s}^{-1}$  of this is estimated to be lost to underflow within the active river bed between the gorge and State Highway One (CRC, 1994), a distance of approximately 40 km. From 1959 to 1981, the greatest number of consecutive days with discharge at the gorge equal to or less than  $150 \text{ m}^3\text{s}^{-1}$  was 181 days in 1977, and the mean was 62 days. Records show an absolute minimum discharge of  $69 \text{ m}^3\text{s}^{-1}$  in July 1982, and a 10 day consecutive minimum of  $90 \text{ m}^3\text{s}^{-1}$  (Bowden *et al.*, 1983). A 10 day sustained low flow  $< 70 \text{ m}^3\text{s}^{-1}$  has a theoretical return period of 50 - 100 years (Bowden *et al.*, 1983). Discharges from the Coleridge power scheme located on a tributary above the gorge, and the Rangitata River diversion scheme below the gorge can alter flows at the gorge by up to  $40 \text{ m}^3\text{s}^{-1}$  diurnally (Sagar & Glova, 1992).

## **Sedimentological regime**

The Rakaia River is usually discoloured by glacial silt and carries a mean yield of  $1640 \text{ tonnes km}^{-2} \text{ yr}^{-1}$  of suspended sediment (Griffiths 1979). Bed load transport to the mouth of the river is difficult to quantify but was estimated by Griffiths (1983) to be approximately 150,000 tonnes of sand and gravel each year. While bed load movement is active at base flow and the river constantly gnaws at banks and obstructions (Rundle, 1985), significant increases in bed load movement occur only at discharges above  $400 \text{ m}^3 \text{ s}^{-1}$  (Mosley, pers. comm., in Sagar, 1986).

## **The active riverbed**

It is important at this stage to mention some of the geomorphological processes that are involved in the formation and maintenance of various habitats within the river. The bedforms and channels are not static, and exist as a result of the hydrological and sedimentological characteristics of the catchment. In the following section, the formation of the braided pattern, seepage streams, and spring streams is discussed, based primarily on the geomorphological descriptions given by Rundle (1985). Technical terms used in this discussion are defined in Table 2. Lastly, the study site and channels are described in detail.

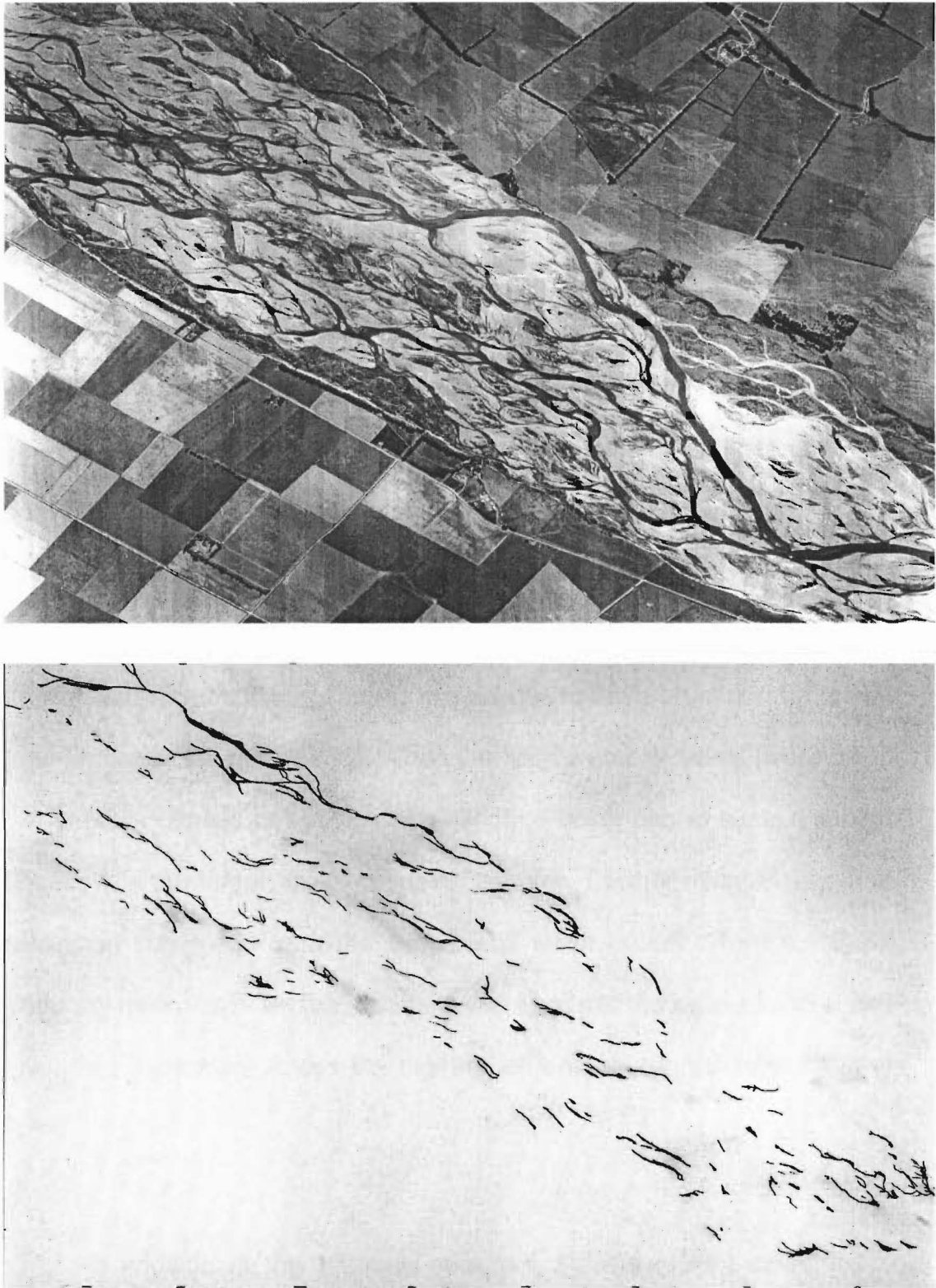


Figure 2. The aerial photograph shows the Rakaia River above State Highway 1 in 1978, the riverbed is about two kilometres wide at this point and flow is to the right. Beneath, a template shows the typical network of seepage and spring stream microhabitats which were of particular interest in this study.

### **Tributary channel networks**

The tributary network contains seepage streams that range in size from a few metres long above a backwater to several hundred metres in length. In some areas, several tributary networks occur across the width of the Rakaia. An example is shown in Figure 2. During a flood the main channels are overtopped by floodwater. This spilled sheet of flood water covers gravel expanses between the main channels, and starts to re-converge, eventually merging with the main channels downstream. As it does so, it is able to scour out smaller channels removed from the main body of water, these channels being described as 'tributary' to the main flow of water. Subsurface water is considered to have an important role in their formation (Rundle, 1985). When the flood water recedes, river flow to the network ceases but subsurface seepage continues to sustain a high baseflow in the larger, freshly incised, streams. Further maintenance and extension can result from the subsurface water supply (Rundle, 1985). Tributary networks drain the area between bends in the main channel, and are offset diagonally across the riverbed alternately, on the right and the left.

In addition to the tributary networks, Rundle (1985) examined a range of bar types in the Rakaia River for evidence of a braiding mechanism capable of splitting flow into various braids. He concluded that the basic mechanism for stream diversion was from chute channel 'piracy',

and hypothesised that the basic mechanism for braiding was the dissection of an ephemeral structure he called the 'tongue'.

### **Tongue structures**

A tongue is formed during floods and is completely submerged under a sheet of water during development. It stems from some point of concentrated flow, which is generally a deep and confined reach such as a channel confluence. Initiation of a 'tongue' requires the combination of tractive competence in the channel and a sheet of quieter water downstream (Rundle, 1985). During a flood, within the confined reaches, a spoon-shaped depression becomes marked where shooting water scours out the bed. As the water slows and spreads out, this material is redeposited as a lunate 'rim' spreading out across the channel downstream. When the flood stage declines the downstream 'rim' begins to obstruct water flow and to cause a steepening in local water grade. Subsequently, the 'tongue' is dissected by one to several 'chute' channels in a manner similar to gully erosion. Sufficiently large floods were observed by Rundle to build 'tongues' larger than the channel from which they originated. As a consequence, the dissecting 'chute' channels were then able to redistribute the water elsewhere across the riverbed. Rundle (1985) contended that in the absence of flooding, the sum effect of otherwise eroding bar forms was to gather sediment into the main

channels. Ultimately, their gradual erosion, would act to reduce the lateral spread of the stream and destroy its braided character.

Table 2. Geomorphological and hydrological terms defined.

<b>Baseflow</b>	The groundwater inflow in the absence of precipitation (Bowden <i>et al.</i> , 1983).
<b>Chute Channel</b>	A steep swift flowing channel that in action is analogous to gully erosion, and involves rapid headward extension. Slumping at the head fall is common and spring sapping by pore pressure due to water between the pebbles is important. If such a gully head penetrates upstream to deep water, the resulting flow scours out the chute and diverts the tapped stream (piracy). Chute channels are the basic mechanism for stream diversion (Rundle, 1985).
<b>Floodplain</b>	Generally vegetated, horizontal bedforms occurring within or adjacent to the active riverbed and periodically inundated by overbank flow (Reinsfeld & Nanson, 1993)
<b>Flood Sheet</b>	Floodwater that originates from overbank flow from the main channel and spreads out as a shallow sheet covering bars and terraces and if large enough, floodplains (Rundle, 1985)
<b>Piracy</b>	Stream diversion resulting from successful capture of upstream flows by a developing chute channel.
<b>Point bar</b>	One of a series of low arcuate ridges of sand and gravel developed on the inside of a growing meander by the slow addition of individual accretions accompanying migration of the channel toward the outer bank (Soons & Selby, 1982).
<b>Shoal reach</b>	Reach of the river where the water shallows and widens over broad gravel bars associated with upstream margins of chute channels and 'tongues'.
<b>Tongue</b>	A constructional bedform that occurs during flood conditions. The tongue form results from the dispersion of contained flow on entering quieter water. Channelized flow results in scouring and high rates of sediment transport from upstream sediment sources, but as the tractive competence diminishes in the spreading flow downstream, the bed load is re-deposited in the form of a lunate bar (Rundle, 1985).

In Figure 3 the formation of a spring stream is summarised based on Rundle's descriptions, and observations that I made on the development of several spring streams over the course of a year. The

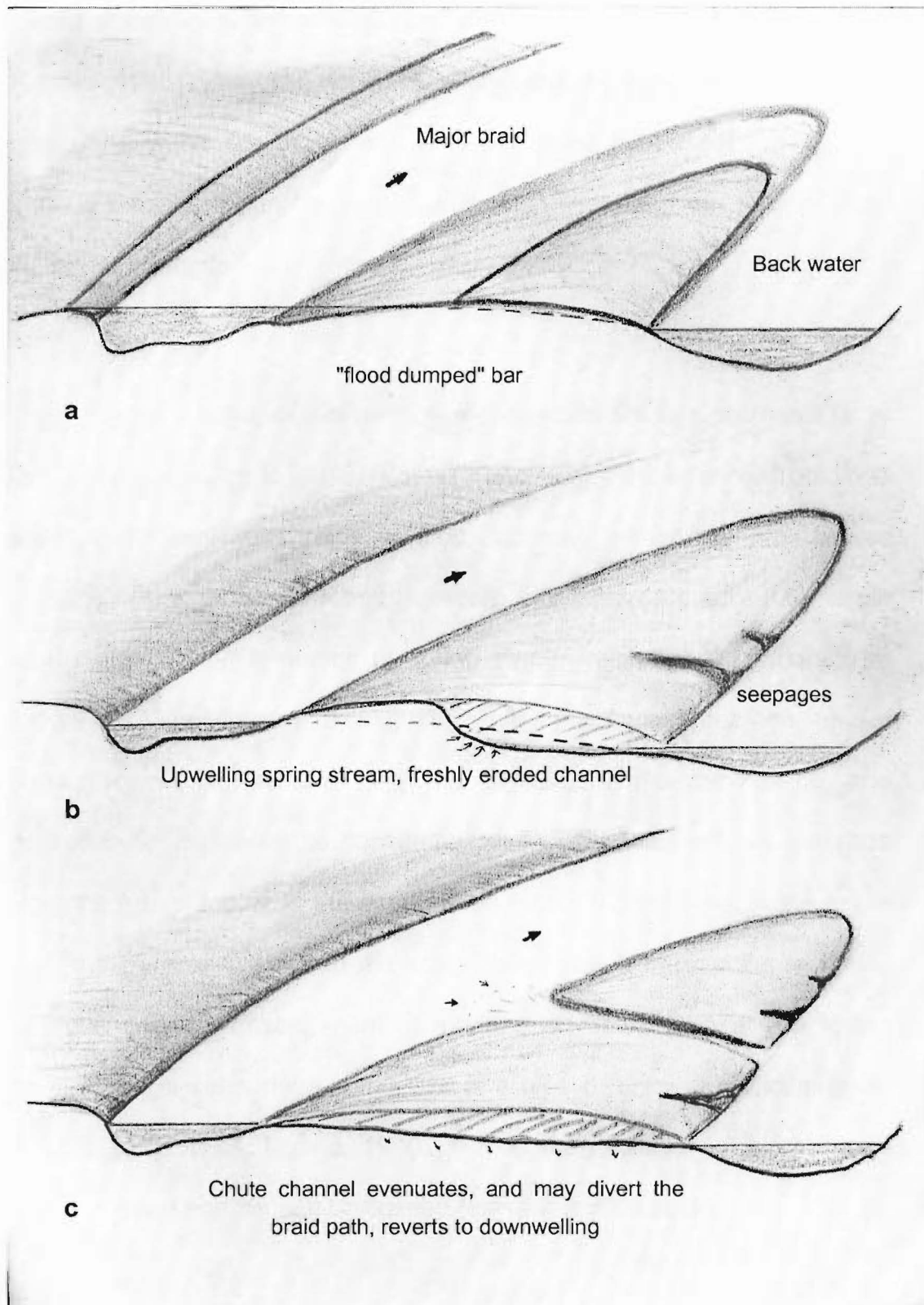


Figure 3. Development of a spring stream. (a) During a flood, bed material is mobilised and redeposited as a large bar. (b) Spring flow in conjunction with surface flow during smaller freshes erodes material at the spring head, a scarp face retreats upstream forming a channel containing a spring stream (c) Eventually chute channels develop which may alter the course of the river.

spring streams are essentially the 'stalled chute channels' described by Rundle (1985). They are not necessarily confined to a 'tongue' and also may occur within the gravel expanses alongside major braids where the various meanders can be 'short circuited' to straighten the path of flood water, for example.

During a flood, bed material is mobilised and redeposited as a large bar (Figure 3a). Due to bank collapse induced by surface scour from flood sheet water and subsurface erosion, incisions are made into the lee margins of these bars. A retreating scarp face upstream from the margin then results in the formation of spring stream microhabitat (Figure 6 a; Figure 3 b). In Figure 6 b, located within the tributary net, the flow of subsurface water has been sufficient to result in the removal of sand draped over the lee of the bar during the last fresh, to remove the sand from the gravel matrix at the spring head (see exposed bank to the left in Figure 6 b), and to steepen the scarp face through bank collapse. Bank collapse and the development of a retreating scarp face at the spring head, through subsurface water flow is a type of erosion called sapping (e.g. Higgins, 1984; Dunne, 1990). During the formation of such spring streams, sand and silt can be flushed from the sediments.

In the absence of the conditions that form bars, those present, including their spring streams and seepages may eventually be incised and transported downstream by a series of chute channels cutting across



the bar (Figure 3 c). Since both flood frequency and flood magnitude are generally greater in spring - summer (Bowden *et al.*, 1983) and significant increases in bed load transport can occur above  $400 \text{ m}^3\text{s}^{-1}$  (Mosley, cited in Sagar, 1986), it is probable that large bar units are generally deposited during large flood events of summer, and reworked by lower and less variable flows in winter.

## Study Site

The study site at Barrhill was about one kilometre wide and 3 km long. The Barrhill site is approximately 25 km above State Highway One and a similar distance below the gorge. Its position in the catchment is shown in Figure 1. The main braid was located about one kilometre from the southern margin of the riverbed. There were several relatively accessible channels and a tributary network containing seepage flow between the terrace and the main braid. This network included a range of seepage and spring streams of various ages, and degrees of isolation. Within the network I chose three distinct types of stream to study in addition to two size classes of braid. These five types of habitat are described in detail in the following sections.

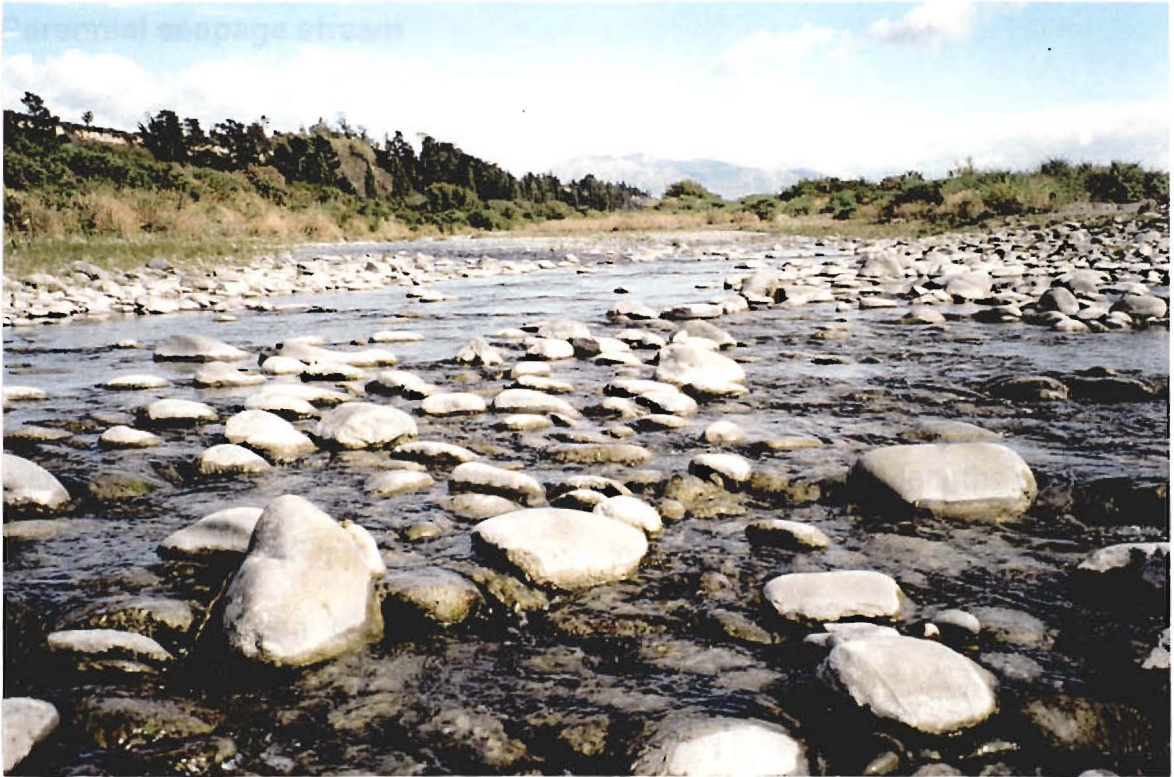


Figure 4. Perennial seepage stream within a tributary network, note the thick algal growth.



Figure 5. Baseflow seepage stream within a tributary network, scour to the left of photograph gives an indication of the depth of recent flood water.

## Perennial seepage stream

Within the study area, perennial seepage streams occurred mainly on the flanks of vegetated floodplain terraces. They formed part of the tributary network and were at sufficiently low elevation to intersect the water table. Here, seepage occurred over extended lengths of stream bed. The study streams had sustained flows throughout their lengths over the study period (Figure 4), although in some cases flow could be observed alternating between the surface and subsurface along the channel.

Three factors indicated that these sites could persist for several years without major changes in their location as a result of flooding. First, they were flanked by vegetated floodplain on at least one, if not both margins. Second, they were generally the only sites containing appreciable numbers of invertebrates with a one year or longer life history. Mature larvae of *Archichauliodes diversus* for example require two to three years to reach their full size and were restricted to this type of stream. Thirdly, perennial seepage streams existed in armoured, and generally silt - bound channels. Rust (1970) regarded channels that had vegetated margins and high proportions of silt and clay in their banks as resistant to lateral erosion.

Silt was most apparent in pools between the riffles. The pools appeared to act as sediment traps, and may have had a role in minimising siltation in

the adjacent riffles. They were relatively devoid of invertebrates. Riffle substrata ranged from armoured cobbles and boulders, to loose gravel and cobbles. Some of the larger cobbles and boulders supported extensive algal mats. Since they still received flow during freshes and floods these sites were clearly vulnerable to siltation, but contained pristine, subsurface - derived water for extended periods, once disconnected from river flow. Seepage could be observed most markedly on the margin nearest to the central riverbed indicating that the water table was highest beneath the minor and major braids, and sloped towards the lower elevation seepage channels in the tributary network.

### **Baseflow seepage stream**

Baseflow seepage streams were essentially minor braids at times of elevated flow, but reverted to seepage streams at baseflow (Figure 5). Their location within the tributary network varied greatly over the year. In winter months they remained relatively unchanged and were predominantly seepage fed. During summer, many but not all became minor braids. The site shown in Figure 5 was a minor braid in summer, but reverted to seepage - fed in winter. Baseflow seepage streams contained patches of loose clean gravels, and patches of armoured cobble / boulder substrata. Silt and sand were less visible within their channels than in perennial seepage streams. They were differentiated from the latter on the basis of their more transient occurrence, more frequently scoured surfaces, and less silted beds.

### **Baseflow spring stream**

Baseflow spring streams were derived from strongly flowing springs in the central river bed. They occurred at locations of lower elevation than nearby major braids. In some sandy pool areas their beds could be observed to "boil". An example of a baseflow spring stream is shown in Figure 6 a - e, and a typical spring head is shown in Figure 6 b. Some of these sites were representative of 'stalled chute channels' as defined by Rundle (1985), and were located outside the main tributary network. Baseflow spring streams were uncommon in some months.

During March, no spring stream habitats were present at the study site, although typically a new spring stream was formed at the study site every 1 - 2 months. The location of baseflow spring streams meant that their disturbance regime approached that of the major braids. They were the most likely channels to contain an extended interstitial habitat since they were located in areas where the bed was continually being reworked by individual flood events. On some occasions they also contained well sorted cobbles and gravels and lacked the otherwise typical fine sand 'packing' near to the surface. This condition is shown clearly in Figure 6 b. Figure 6 e shows that these sites are also vulnerable to sand deposition during moderately small freshes.





Figure 6 a. Baseflow spring stream, 'stalled chute channel', note the pristine water quality.



Figure 6 b. Baseflow spring head, note the ripples along the water surface which give an indication of the velocity of the emerging water, gravels at the spring head contained a relatively high quantity of particulate organic matter, and sometimes contained high numbers of early instar *Deleatidium* larvae.





Figure 6 c. Backwater, note location of spring head left of centre, the mouth of the spring stream was to the left of the photograph.



Figure 6 d. Braid confluence looking back towards backwater, major braid in background is clearly at a higher elevation, flow is from left to right.





Figure 6 e. A small fresh deposited sand within this former spring stream, small *Deleatidium* larvae and *Phreatogammarus fragilis* were retrieved from 400 mm deep six weeks prior.



Figure 7. Major braid, note the band of filamentous algae in shallow water, indicating a brief period of stable discharge during summer.



## **Braids**

Rundle (1985) described the main channel segments of the Rakaia as sinuous, and the side channels as relatively stable creeks, frequently fed by spill from the outer bends of the main channels. Rundle (1985) recognised a general tendency for braids in the Rakaia River to meander at baseflow. The larger river channels in the Rakaia River have a width - depth ratio of about 20 : 1 but shoal reaches may have a ratio ten times as high (Rundle, 1985). Constant side slopes are present where there is undercutting. Vertical banks occur above the water level where substantial amounts of sand are packed between boulders, but this material slumps immediately if it is saturated (Rundle, 1985). These conditions are found on the outsides of bends, whereas the inside bank slope is more gentle and runs out as a 'point bar' (Rundle, 1985). In Figure 7, a band of filamentous algae can be seen along the shallow margin indicating a period of extended stable flow has occurred.

## CHAPTER 3

### SECONDARY PRODUCTION

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#### Invertebrate fauna of braided rivers

Braided rivers on the east coast of the South Island are characterised by frequent flooding, high sediment loads, and physically unstable beds (Bowden *et al.*, 1983; Sagar, 1986; Rundle, 1985). Like the mountain streams in their headwaters, they can be considered to be physically dominated systems in which biological interactions take a secondary role (e.g., Cowie, 1980; Graesser, 1988; Winterbourn *et al.*, 1981; Winterbourn, 1997). Their invertebrate communities are highly resilient to flooding (Scrimgeour *et al.* 1988; Sagar, 1986) and dewatering of channels (Sagar, 1983a).

The diversity of aquatic invertebrates inhabiting this type of river is quite low (Sagar, 1986; Scrimgeour, 1987). Larvae of *Deleatidium* spp. (Ephemeroptera), *Hydrobiosis* spp. (Trichoptera), *Hydora* sp. (Coleoptera), and *Aoteapsyche* spp. (Trichoptera) (Scrimgeour *et al.*, 1988), along with Chironomidae (Diptera) and Tipulidae (Diptera) (Sagar, 1986) comprise a common nucleus of taxa in South Island braided rivers. These faunas are affected most notably by flood discharges that exceed the threshold of flow inducing significant increases in bed movement

(Sagar, 1986; Scrimgeour & Winterbourn, 1989). The frequent numerical dominance of *Deleatidium* in these physically harsh environments reflect the strong colonising ability of this mayfly, its refuge seeking behaviour during spates, and generalist feeding and habitat requirements (Winterbourn, 1997). Such characteristics are common to numerous taxa in New Zealand mountain stream communities, which Winterbourn (1997) argued were stable in species composition in the long term despite many streams having physically unstable beds, variable and unpredictable discharge patterns, and changing vegetational settings. Scrimgeour *et al.*, (1988) noted that refuge areas, refuge seeking behaviours, the ability to recolonise previously denuded substrates rapidly, and various life history traits such as extended flight and emergence periods probably all help to minimise the effects of flood events on invertebrate populations.

Few studies have attempted to measure secondary production in braided rivers, and to do so, a wide range of habitats need to be considered and incorporated into calculations. In this chapter, calculations and secondary production of the most common invertebrate species living in various braids and seepage streams of the Rakaia are provided and discussed.

It can be argued reasonably that production is the most comprehensive representation of "success" for a population because it is a composite of most other components of success, including density, biomass, individual growth rate, reproduction, survivorship, and

development time (Benke, 1984). In an applied sense it is a more accurate measure of the food that is available to fish and bird species utilising various habitats than is dry weight alone. Average dry weights of invertebrates collected from the Waimakariri and Ashley Rivers in a study by Hughey *et al.* (1989), and from a past study on the Rakaia by Pierce (1979), was also used to estimate production by multiplying them by production / biomass rates obtained in this study. This enabled a comparison to be made between production in several Canterbury foothill and alpine catchment rivers, differing in size and hydrologic regime.

## Methods

Four quadrats were located randomly within 10 metre sampling transects along riffles in a perennial seepage stream (discharge  $< 1 \text{ m}^3 \text{ s}^{-1}$ ), a baseflow seepage stream ( $< 1 \text{ m}^3 \text{ s}^{-1}$ ), a baseflow spring stream ( $< 1 \text{ m}^3 \text{ s}^{-1}$ ), and in minor ( $< 10 \text{ m}^3 \text{ s}^{-1}$ ) and major braids ( $> 40 \text{ m}^3 \text{ s}^{-1}$ ). Riffles were sampled at approximately six weekly intervals from October 1997 to August 1998, at baseflow, with no riffle sampled more than once. When channel migration eliminated or altered channels under study, sites with similar physical characteristics were substituted. This effectively meant that samples were taken from two separate perennial seepage streams, three baseflow seepage streams, seven baseflow spring streams, seven minor braids, and two major braids during the course of the study. However, samples were grouped into one of each of the five basic channels to estimate production.

Invertebrates were collected with a triangular stream net (0.1 - 0.3 mm mesh, 300 mm sides) held behind a 300 mm by 300 mm quadrat in ankle-deep water. Stones were carefully moved downstream of the frame so the stream net could be bedded into sand. Larger stones were either held inside the net or placed in a bucket before invertebrates and algae were brushed from them. The remaining substrate was disturbed to a depth of 100 mm using a 10 mm diameter steel rod. Invertebrates were preserved in the field with 70% methanol and later sorted in a Bogorov tray at 10X magnification. Identifications were made at magnifications between 10X and 160X using the keys and descriptions of Cowley (1978), McFarlane (1951, 1975), Winterbourn (1973), and Winterbourn & Gregson (1989).

### Calculation of production

Secondary production was calculated with the size frequency method (Benke, 1984) for Deleatidium spp. (Ephemeroptera), Hydrobiosidae (Trichoptera), Pycnocentroides aureola (Trichoptera), Aoteapsyche spp. (Trichoptera), Zelandobius furcillatus (Plecoptera), Elmidae (Coleoptera), and Chironomidae (Diptera). The basis of this method is the calculation of an average cohort. For each size class of a taxon, the annual mean density is calculated from samples taken throughout the year. This is an approximation of survivorship over the year, in which animals are assumed to have spent an equal length of time

in each size category. Production of the average cohort is first calculated as the number of individuals lost (presumably to mortality) between successive size categories. These losses are given a biomass value by multiplying the number of individuals lost by the average weight of successive size classes. This represents a loss in population biomass, and the sum of all biomass losses is an approximation of average cohort production. To obtain annual production it is assumed that there are the same number of average cohorts as size classes, therefore average cohort production is multiplied by the number of cohorts (Benke, 1984). Negative values in the final summation were excluded as recommended by Benke & Wallace (1980).

Body lengths of all invertebrates were measured ( $\pm 0.05$  mm) and converted to dry weight (DW). For *Deleatidium*, the equation provided by Huryn (1996b) was used, and the units of AFDM were converted to DW by dividing by 0.85 (Whiles & Wallace, 1995). For Chironomidae, the equation of Smock (1980) which grouped Chironominae and Orthocladiinae was used. Equations from Towers, Henderson & Veldtman (1991) were used for the remaining invertebrates. Their regression equation for *Zelandobius furcillatus* was found to be incorrect, however, so their general equation for Plecoptera was used instead. A correction for unequal sampling interval was included in all calculations following Krueger & Martin (1980). Frequent flooding disrupted sampling in both

summer and early spring so that some collections were made up to two weeks after the planned date.

Flooding reduced the overall period sampled to 300 days as collections could not be made in September, the last month planned for field work. Flooding also resulted in incomplete sampling during January, when collections were taken only from a minor braid, major braid, and a baseflow spring stream. Many of the common invertebrates, such as *Deleatidium* spp. and Chironomidae typically exhibit aseasonal life histories (Winterbourn, 1973; Cowie, 1980; Boothroyd, 1988), so loss of the September period from the sampling regime probably had little effect on calculation of the average cohort. The 'coarse' six weekly sampling regime used, was considered adequate to estimate production because of the characteristic aseasonality of the fauna, and the predominance of early instar larvae of most species throughout much of the year. This interval was chosen for logistic reasons: the sorting of more frequent collections would have been prohibitive.

Annual production estimates were corrected to take account of cohort production intervals (CPI) following Benke (1979). The CPI correction used for *Deleatidium* spp. was 1.93 based on my best estimate of its life history as indicated by Figure 10. Average cohort length was about 190 days based on this dataset. Chironomidae were assumed to be mainly species of Orthocladiinae based on the results of a year long study

in the Rakaia by Sagar (1986) and the examination of a sub-sample of larvae in this study. The latter demonstrated the presence of *Naonella* (Orthoclaadiinae) and *Cricotopus* sp. (Orthoclaadiinae), which are likely to have similar life histories (M. J. Winterbourn, pers. comm.), and also *Tanytarsus* sp. (Chironominae: Tanytarsini). The CPI correction (2.65) used for Chironomidae was based on the mean CPI for Orthoclaadiinae in Stony Creek, Otago (range 0 °C to 16.5 °C, mean 6 °C) estimated by Huryn (1998) to range from 93 to 182 days. Winter temperatures at Huryn's study sites were between 0 °C and 3 °C, and were lower than those in the Rakaia by about 5 °C. My CPI of 2.65 is almost certainly a conservative estimate. A CPI of 210 days was used for *Zelandobius furcillatus* based on an estimate of its life history length (Figure 14). All the remaining invertebrates were assumed to have a larval CPI of 1.09. About 30 days are assumed to be needed for egg, pupal (if present) and adult stages.

Total production of invertebrates was estimated by summing production values for individual taxa. This was possible given that only seven invertebrate groups were present in sufficient numbers to estimate production (Table 3) and all other taxa were rare. Actual total production is probably within the confidence intervals calculated for these seven species combined.



## Estimation of confidence limits for production values

The inclusion of confidence intervals allows unambiguous assessment of differences in production between channel types. Ninety five percent confidence intervals (CIs) were estimated using the bootstrap, a non-parametric resampling technique (Effron & Tibshirani, 1993). Bootstrapping is used to estimate the level of uncertainty of values for variables with unknown or complex frequency distributions, or where logistical restraints have resulted in insufficient replication such as in production studies (Morin et al, 1987). Every data set was bootstrapped by randomly resampling with replacement, one of the four quadrats from each sampling period. Values for average cohorts were recalculated each time, until 1000 production estimates were available for each site and each taxonomic group. These estimates were then ranked and the 25<sup>th</sup> and 975<sup>th</sup> estimate were taken to be the upper and lower 95% confidence intervals, respectively (Percentile method: Effron & Tibshirani, 1993). For Deleatidium and Chironomidae, random CPI values were normally distributed between the minimum and maximum values and included in the bootstrap procedure following Huryn (1998). To estimate confidence intervals for total production, the sum of the 1000 bootstrap production estimates for each group was taken and then ranked.



Table 5. Secondary production in the Rakaia River ( $\text{g DW m}^{-2} \text{yr}^{-1}$ ), with 95% confidence intervals.

[illegible]

## Secondary Production, Rakaia River

Plate 10. Secondary Production

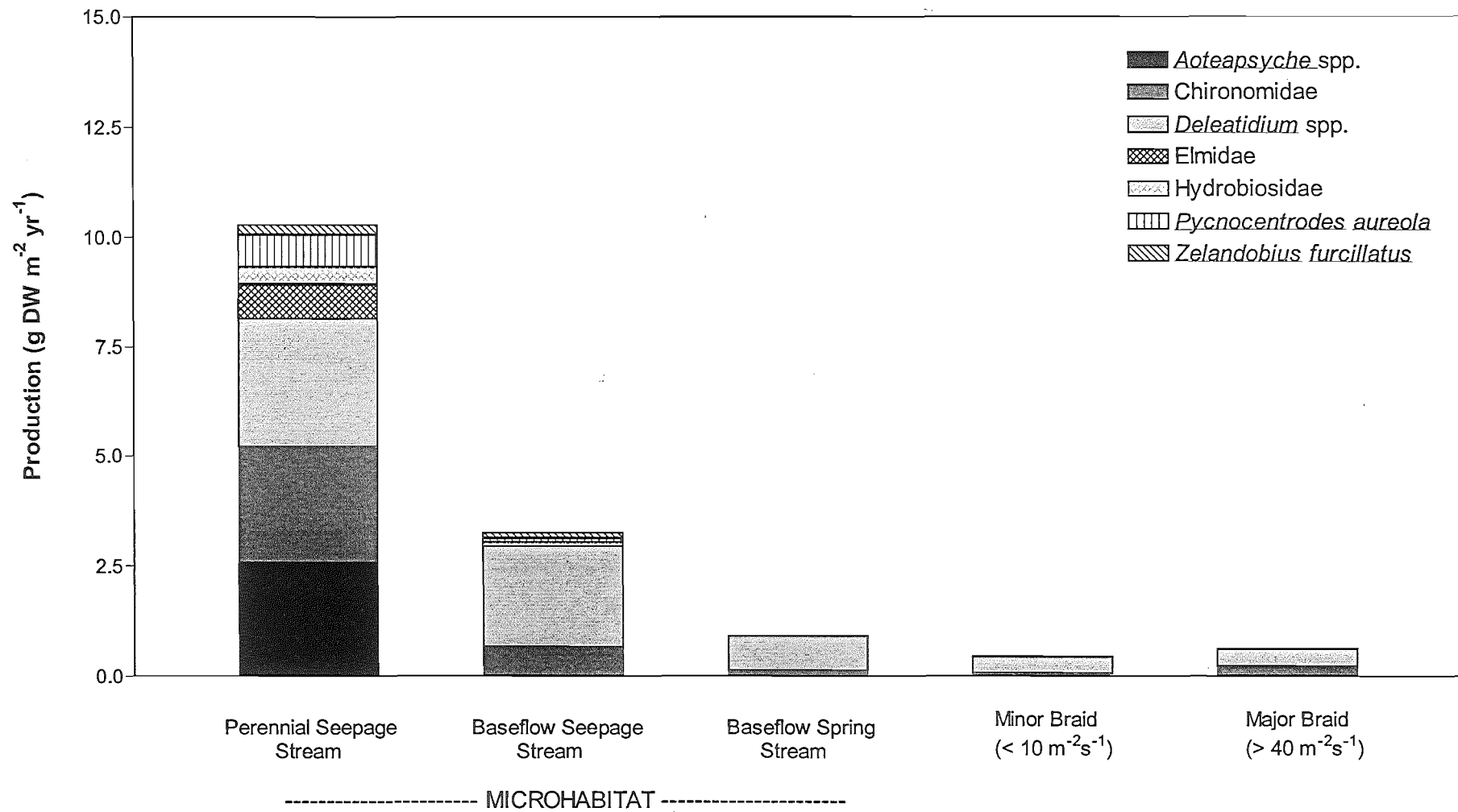


Figure 8. Secondary production in various habitats of the Rakaia River at Barrhill, from October 1997 to August 1998.

## Results

Table 3. Aquatic macroinvertebrates collected from the Rakaia River

GASTROPODA	MEGALOPTERA
Hydrobiidae	Corydalidae
<u><i>Potamopyrgus antipodarum</i></u>	<u><i>Archichauliodes diversus</i></u>
EPHEMEROPTERA	TRICHOPTERA
Leptophlebiidae	Hydropsychidae
<u><i>Deleatidium lillii</i></u> group	<u><i>Aoteapsyche colonica</i></u>
<u><i>Deleatidium myzobranchia</i></u> group	<u><i>Aoteapsyche catherinae</i></u>
PLECOPTERA	<u><i>Aoteapsyche</i></u> sp.
Gripopterygidae	Rhyacophilidae
<u><i>Zelandobius furcillatus</i></u>	<u><i>Hydrobiosis frater</i></u>
<u><i>Zelandoperla decorata</i></u>	<u><i>Hydrobiosis umbripennis</i></u>
COLEOPTERA	<u><i>Hydrobiosis parumbripennis</i></u>
Hydrophilidae	<u><i>Psilochorema bidens</i></u>
<u><i>Berosus</i></u> sp.	Hydroptilidae
Elmidae	<u><i>Oxyethira albiceps</i></u>
DIPTERA	<u><i>Paroxyethira</i></u> sp. (pupa)
Tipulidae	Conoesucidae
Eriopterini sp. A	<u><i>Olinga feredayi</i></u> (pupa)
Eriopterini sp. B	<u><i>Pycnocentroides aureola</i></u>
<u><i>Aphrophila</i></u> sp.	<u><i>Bareoptera roria</i></u>
Chironomidae	Leptoceridae
Orthocladiinae	<u><i>Hudsonema amabilis</i></u>
<u><i>Naonella</i></u>	AMPHIPODA
<u><i>Cricotopus</i></u> sp.	Gammaridae
Chironominae: Tanytarsini	<u><i>Phreatogammarus fragilis</i></u>
<u><i>Tanytarsus</i></u> sp.	<u><i>Paraleptamphopus</i></u> sp.
Ceratopogonidae	COPEPODA
Forcipomyiinae	Cyclopoida
Ceratopogoninae	Calanoida
Simuliidae	
<u><i>Austrosimulium</i></u> australense group	
Empididae	

## Total invertebrate production

Total invertebrate production in the various river channels varied considerably, and is summarised in Figure 8, and Tables 4 and 5. A full set of histograms displaying the bootstrap estimates for total production are given in Appendix 1. Tables summarising production calculations for individual taxa, based on mean densities in each channel type, are included at the end of this chapter as Tables 7 - 23. Calculations based on

the information provided may differ slightly at each stage because of small but cumulative rounding errors.

Total production, estimated for the two types of seepage stream were  $10.3 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , and  $3.2 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , for the 'perennial' and 'baseflow' seepage streams, respectively. In contrast, total production estimated for the baseflow spring stream was only  $1.0 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , and the minor and major braids had lower values of  $0.5 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , and  $0.6 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , respectively. If the 95% confidence limits calculated by bootstrapping do not overlap, values can be considered to be significantly different (Effron & Tibshirani, 1993). On the basis of this criterion, both seepage streams had significantly greater secondary production than all other channel types (Table 4, Figure 8). Production in the baseflow spring stream was not significantly greater than that in the braids but was significantly lower than in the seepage streams. Production in the spring stream, and the braids was not significantly different. The production to biomass ratio was 8 for the perennial seepage stream, and was significantly less than that for the baseflow seepage stream with a P/B ratio of 15. No other P/B ratios were significantly different between habitats (Table 4).

### **Production of Chironomidae**

Chironomid production varied markedly between channel types. The 'perennial' and 'baseflow' seepage streams had production rates of

2.6 g DW m<sup>-2</sup> yr<sup>-1</sup> and 0.7 g DW m<sup>-2</sup> yr<sup>-1</sup>, respectively, whereas chironomid production in the baseflow spring stream was estimated at 0.2 g DW m<sup>-2</sup> yr<sup>-1</sup>. The minor and major braids had calculated values of 0.1 g DW m<sup>-2</sup> yr<sup>-1</sup>, and 0.2 g DW m<sup>-2</sup> yr<sup>-1</sup>, respectively. Statistically significant differences among channels were almost identical to those for total invertebrate production (Table 4), except that chironomid production in the major braid was not significantly lower than that in the baseflow seepage stream. In the perennial seepage stream, chironomid density ranged from 2340 m<sup>-2</sup> in April, to 24530 m<sup>-2</sup> in August 1998 (Figure 9). By comparison, densities ranged from 10 m<sup>-2</sup> to 3870 m<sup>-2</sup> in the baseflow seepage stream. Maximum densities in the baseflow spring stream, minor braid, and major braid were 1000, 350, and 960 m<sup>-2</sup>, respectively. Small larvae were dominant in all months except March and late April, when mid to late instar larvae were present in greater numbers (Figure 9). This probably reflects greater flow stability during these months (Bowden *et al.*, 1983) and therefore survivorship of mid to late instars in these months. Production to biomass rates were not significantly different between sites and ranged from 18 to 22 (Table 4). It was impossible to obtain the life history information for Chironomidae given the coarse sampling interval, although Cowie (1980) considered the life histories of Chironomidae in a West Coast stream to be typically aseasonal as did Boothroyd (1988) in the North Island.

### Production of Deleatidium spp.

Deleatidium (*lillii* group) and Deleatidium (*myzobranchia* group) were present in the study area, but their smaller instar larvae cannot be told apart and no attempt was made to distinguish between them in estimating production. Overall, Deleatidium production was similar in magnitude to that of Chironomidae, but in the 'baseflow' streams, and the 'braids', the contribution of Deleatidium exceeded that of Chironomidae (Table 4). This was significant in all but the major braids (Table 4). Significant differences in production paralleled that for total production, except that the two seepage streams were not significantly different from each other. Estimated Deleatidium production was  $2.9 \text{ g DW m}^{-2} \text{ yr}^{-1}$  and  $2.3 \text{ g DW m}^{-2} \text{ yr}^{-1}$  for the 'perennial' and 'baseflow' seepage streams, respectively. Production in the baseflow spring stream was  $0.8 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , whereas the minor and major braids had lower estimated values of  $0.3 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , and  $0.4 \text{ g DW m}^{-2} \text{ yr}^{-1}$  respectively. Production to biomass ratios were approximately 14 in the seepage streams, a value typical of a bivoltine insect (Table 4).

Larval density also varied among the streams and braids (Figure 10). It ranged from  $500 \text{ m}^{-2}$  to  $1872 \text{ m}^{-2}$  in the perennial seepage stream,  $75 \text{ m}^{-2}$  to  $2214 \text{ m}^{-2}$  in the baseflow seepage stream,  $275 \text{ m}^{-2}$  to  $889 \text{ m}^{-2}$  in the baseflow spring stream,  $39 \text{ m}^{-2}$  to  $394 \text{ m}^{-2}$  in the minor braid, and from  $8 \text{ m}^{-2}$  to  $208 \text{ m}^{-2}$  in the major braid. The second lowest density of Deleatidium larvae in the perennial seepage stream ( $603 \text{ m}^{-2}$ ) occurred in



October 1997, when the highest overall density was also recorded in the baseflow seepage stream ( $2210 \text{ m}^{-2}$ ) (Figure 10). The high density found in the baseflow seepage stream was notable because it is almost 4 times greater than the density in the perennial seepage stream, which had relatively much higher densities of *Aoteapsyche* spp., Hydrobiosidae, and *Pycnocentroides aureola*. Also it was almost ten times greater than the density in the 'braids' where few invertebrates other than Chironomidae or *Deleatidium* spp. occurred. Size frequency distributions indicated a predominance of early to mid instar larvae at all the sites. During months of frequent flooding, for example December 1997 (Figure 10), the proportion of later instars of *Deleatidium* spp. appeared to be better represented than mid to late instars of Chironomidae (Figure 9).

The life history data for *Deleatidium* spp. indicated a period of rapid growth during summer followed by a period of slower growth during winter (Figure 10). Larvae hatching in February probably matured by mid September; i.e., in approximately 36 weeks. Those hatching in September probably emerged in January, that is in approximately 24 weeks. Figure 10 provides clear evidence of rapid growth during October and December 1997, although the life history information was then truncated because of flooding. The 24 week estimate was based on extrapolation of the growth curve for this summer generation. It is likely to be an over estimate of the absolute minimum cohort generation time as Huryn (1996) found that *Deleatidium* hatching from eggs deposited before mid February in an

Otago high country stream, had probably emerged as adults before May (minimum cohort duration  $\approx$  3 months).

### Production of Aoteapsyche spp.

At least three species of Aoteapsyche were present, but Aoteapsyche colonica and A. catherinae were the most common. Mature pupae were also identified for A. colonica and A. catherinae. An uncommon species that keyed most closely to A. raruraru was also present. Fifth instar larvae and pupae of A. catherinae outnumbered A. colonica 2:1. A. catherinae is usually associated with gently - flowing streams where clay and silt form a considerable proportion of the substrate (McFarlane, 1976). My production estimates were for larvae of all species grouped together. Aoteapsyche were restricted largely to the perennial seepage stream, where larval densities ranged from 43 m<sup>-2</sup> to 389 m<sup>-2</sup> (Figure 11), and estimated production was 2.6 g DW m<sup>2</sup> yr<sup>-1</sup> (Table 4). The production to biomass rate was approximately 4 (Table 2). The other sites were almost devoid of Aoteapsyche except that small larvae inhabiting filamentous algae were recorded from a major braid (Figure 6) during March 1998, where they had a mean density of 83 m<sup>-2</sup>. Larvae were recruited throughout the year (Figure 11). The CPI of 335 days used may have underestimated annual production as winter temperatures were up to 9 °C during the day, and may have supported moderately rapid growth.

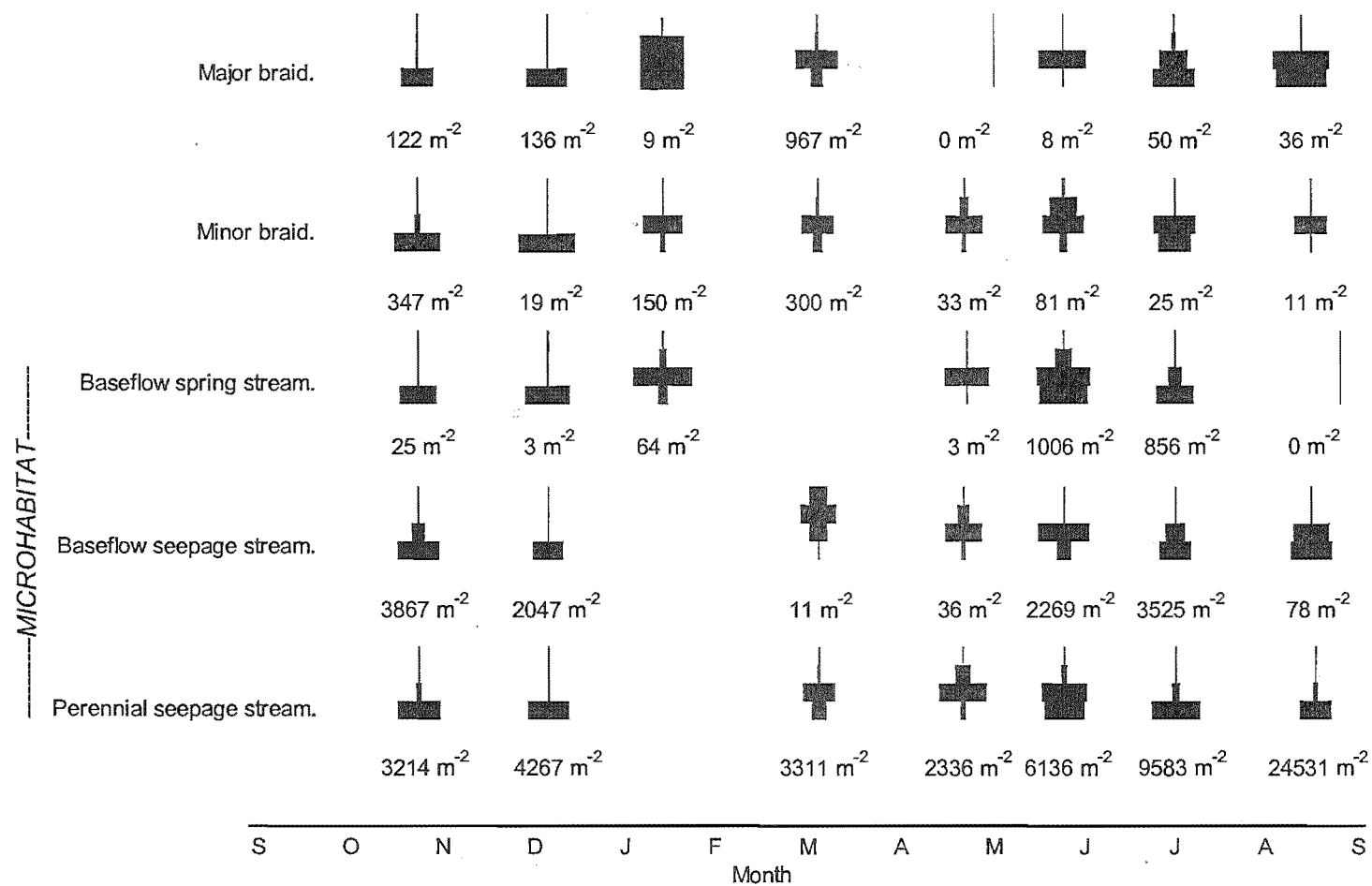


Figure 9. Size - frequency distributions and mean densities of Chironomidae in the five habitats over the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 2 mm; 2 - 4 mm; 4 - 6 mm; 6 - 8 mm (the scale of the bars varies between graphs).

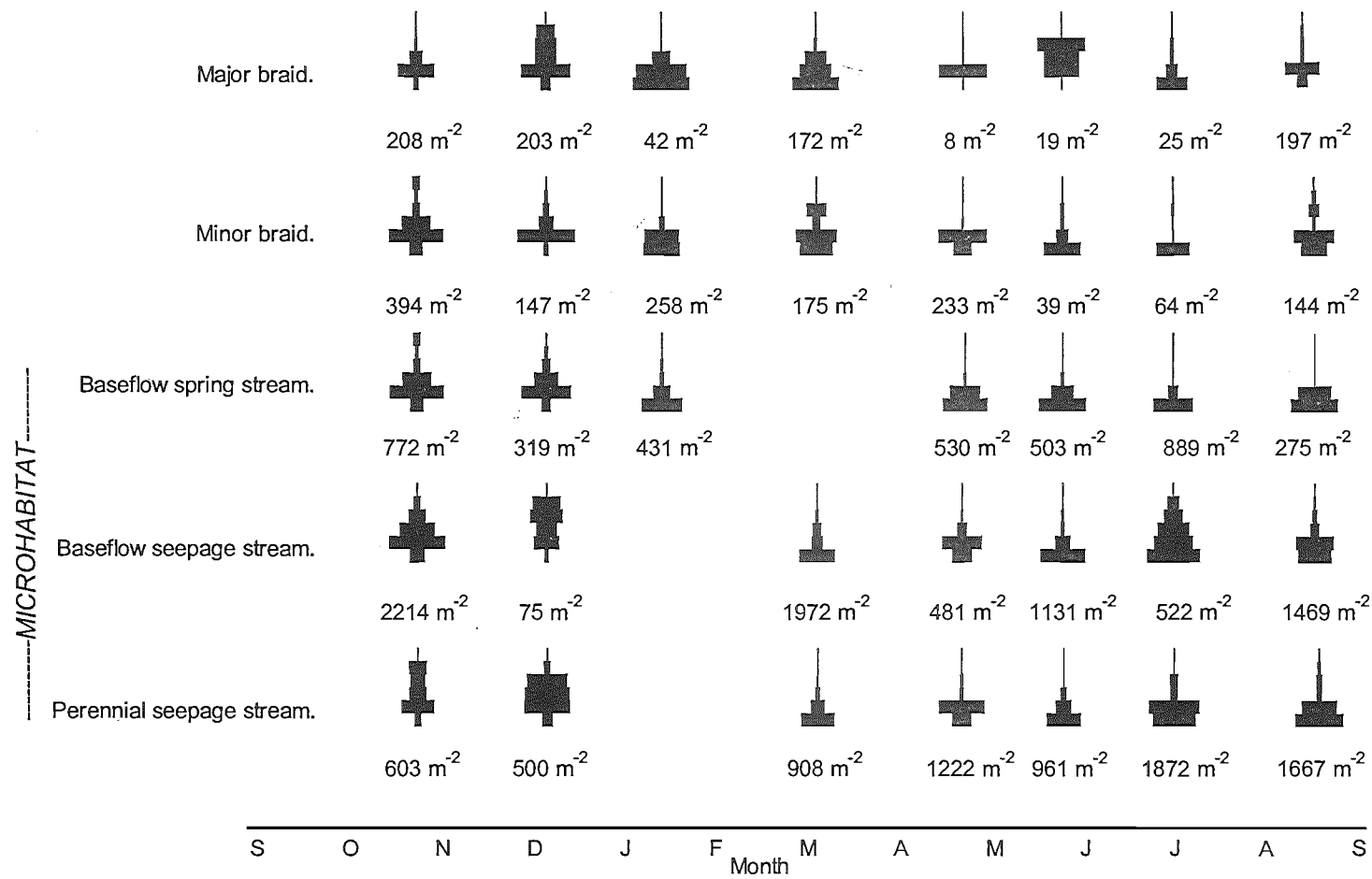


Figure 10. Size - frequency distributions and mean densities of *Deleatidium* spp. in the five habitats over the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 2 mm; 2 - 4 mm; 4 - 6 mm; 6 - 8 mm; 10 - 12 mm (the scales of the bars varies between graphs).

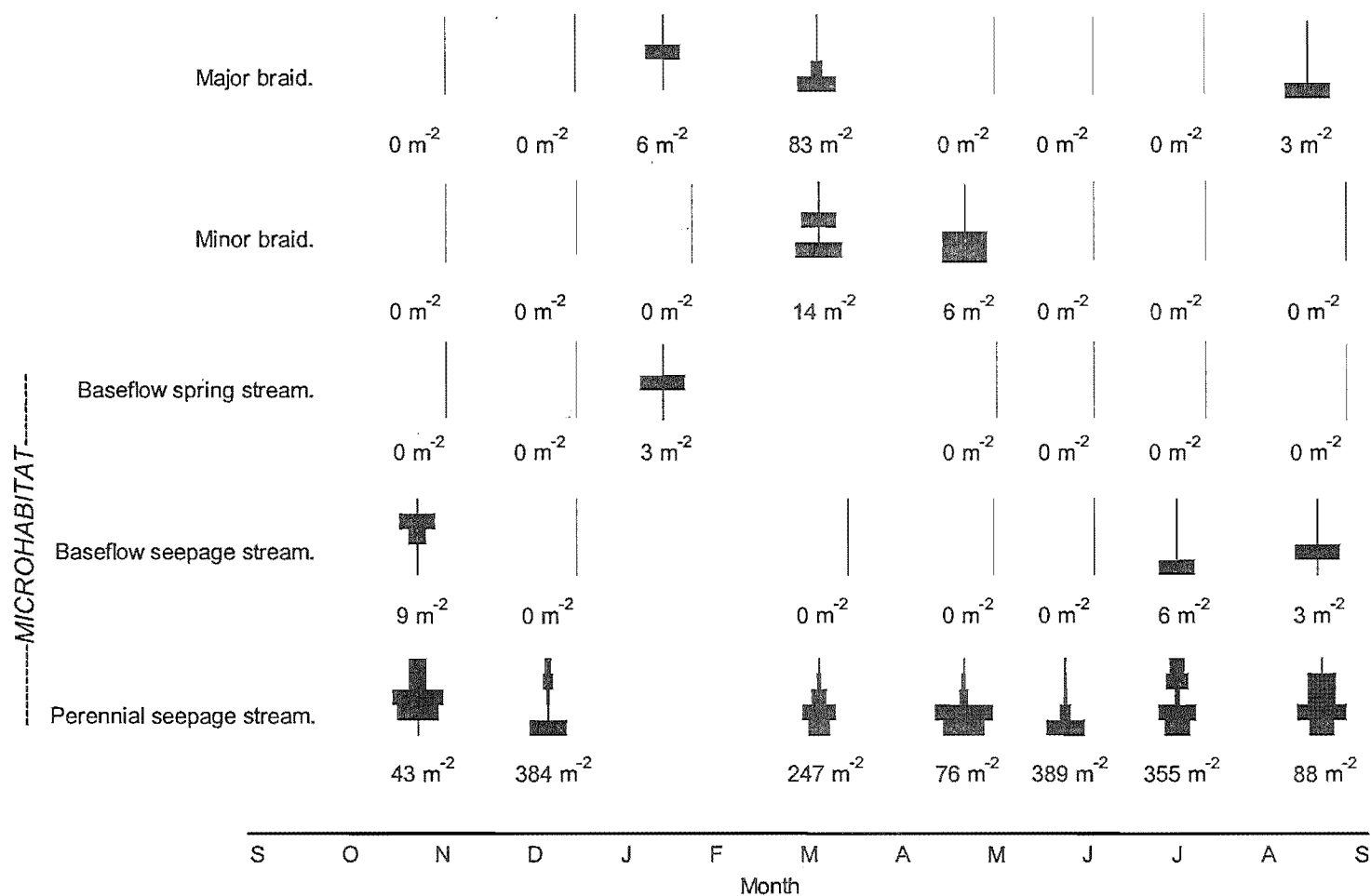


Figure 11. Size - frequency distributions and mean densities of *Aoteapsyche* spp. in the five habitats during the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 4 mm; 4 - 8 mm; 8 - 12 mm; 12 - 16 mm; 16 - 20 mm (the scale of the bars varies between graphs)

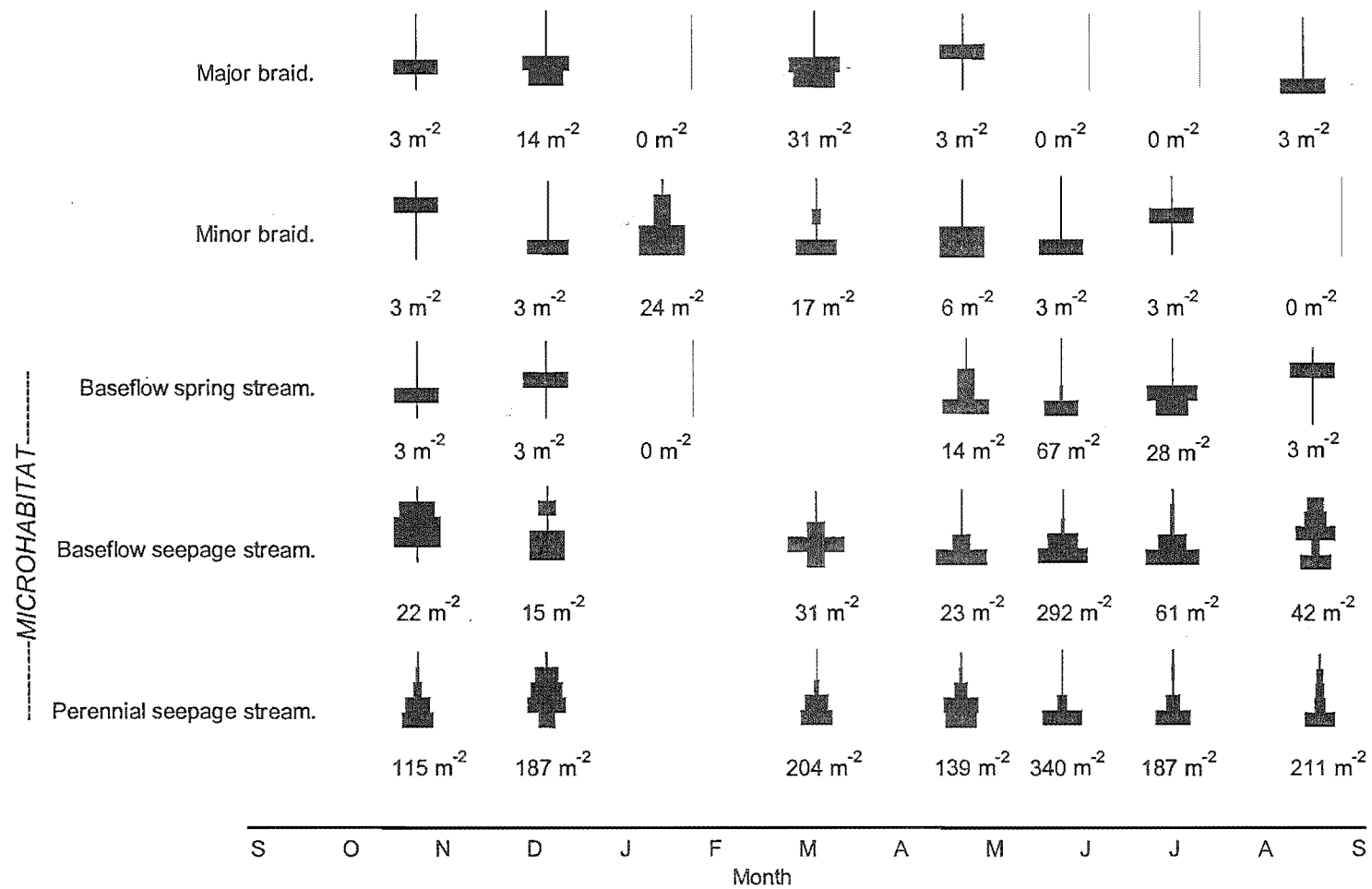


Figure 12. Size frequency distributions and mean densities of Hydrobiosidae in the five habitats over the study period. In the graph, the bars from the bottom to the top represent the size classes: 0 - 4 mm; 4 - 8 mm; 8 - 12 mm; 12 - 16 mm; 16 - 20 mm (the scale of the bars varies between graphs).

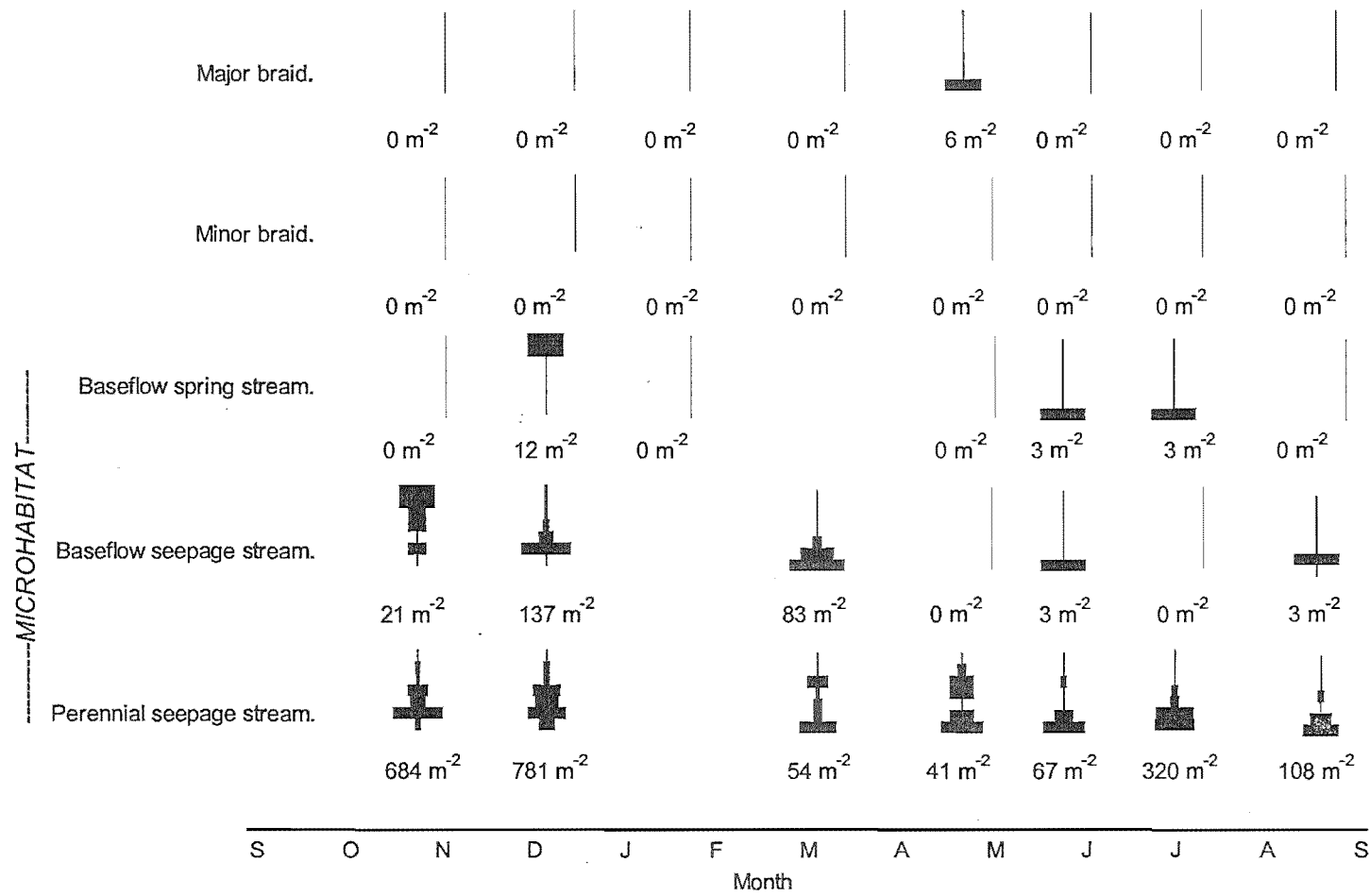


Figure 13. Size frequency distributions and mean densities of *Pycnocentroides aureola* in the five habitats over the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 2 mm; 2 - 4 mm; 6 - 8 mm; 8 - 10 mm; 10 - 12 mm (the scale of the bars varies between graphs).

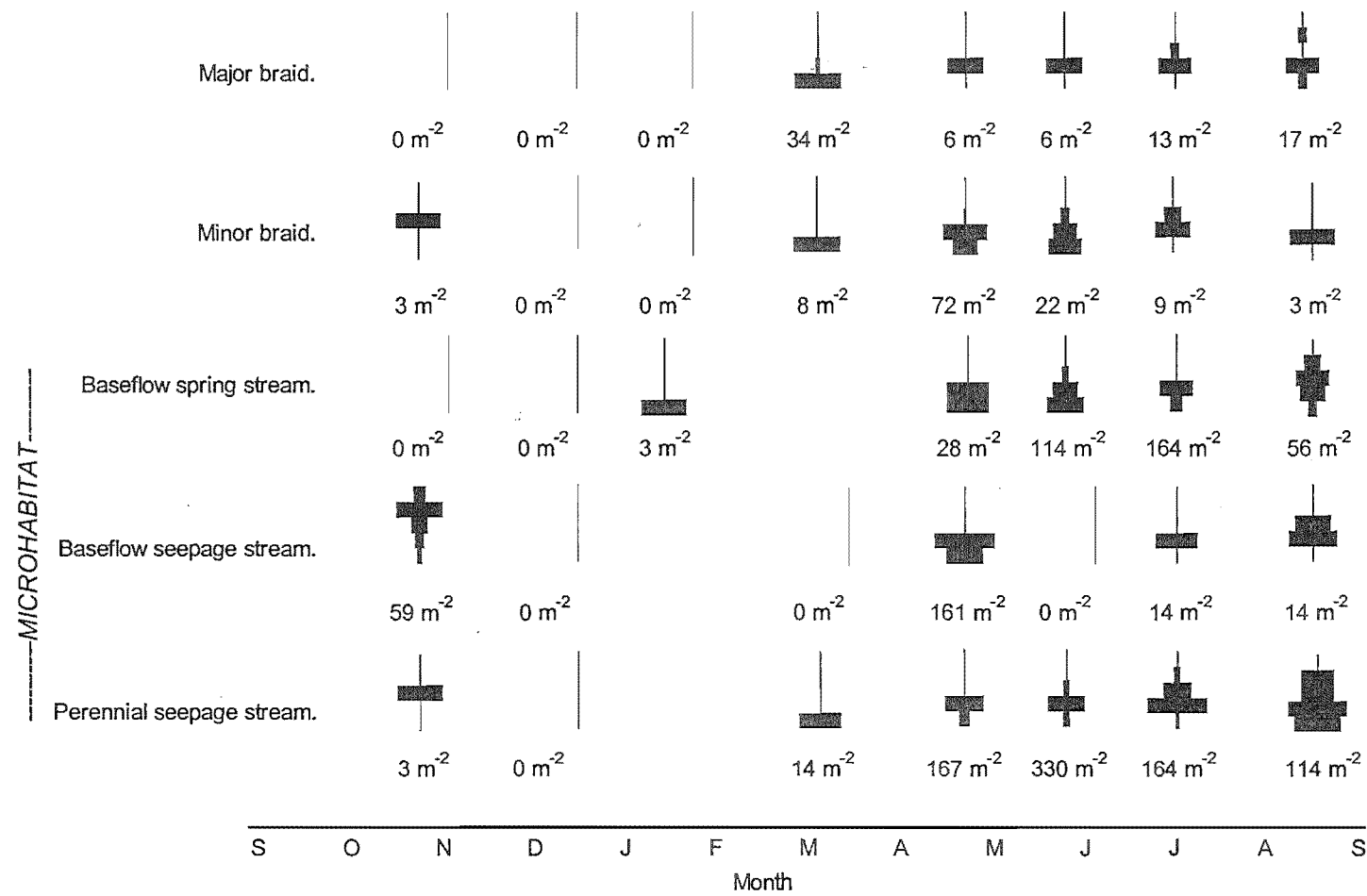


Figure 14. Size frequency distributions and mean densities of *Zelandobius furcillatus* in the five habitats over the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 2 mm; 2 - 4 mm; 4 - 6 mm; 6 - 8 mm (the scale of the bars varies between graphs).



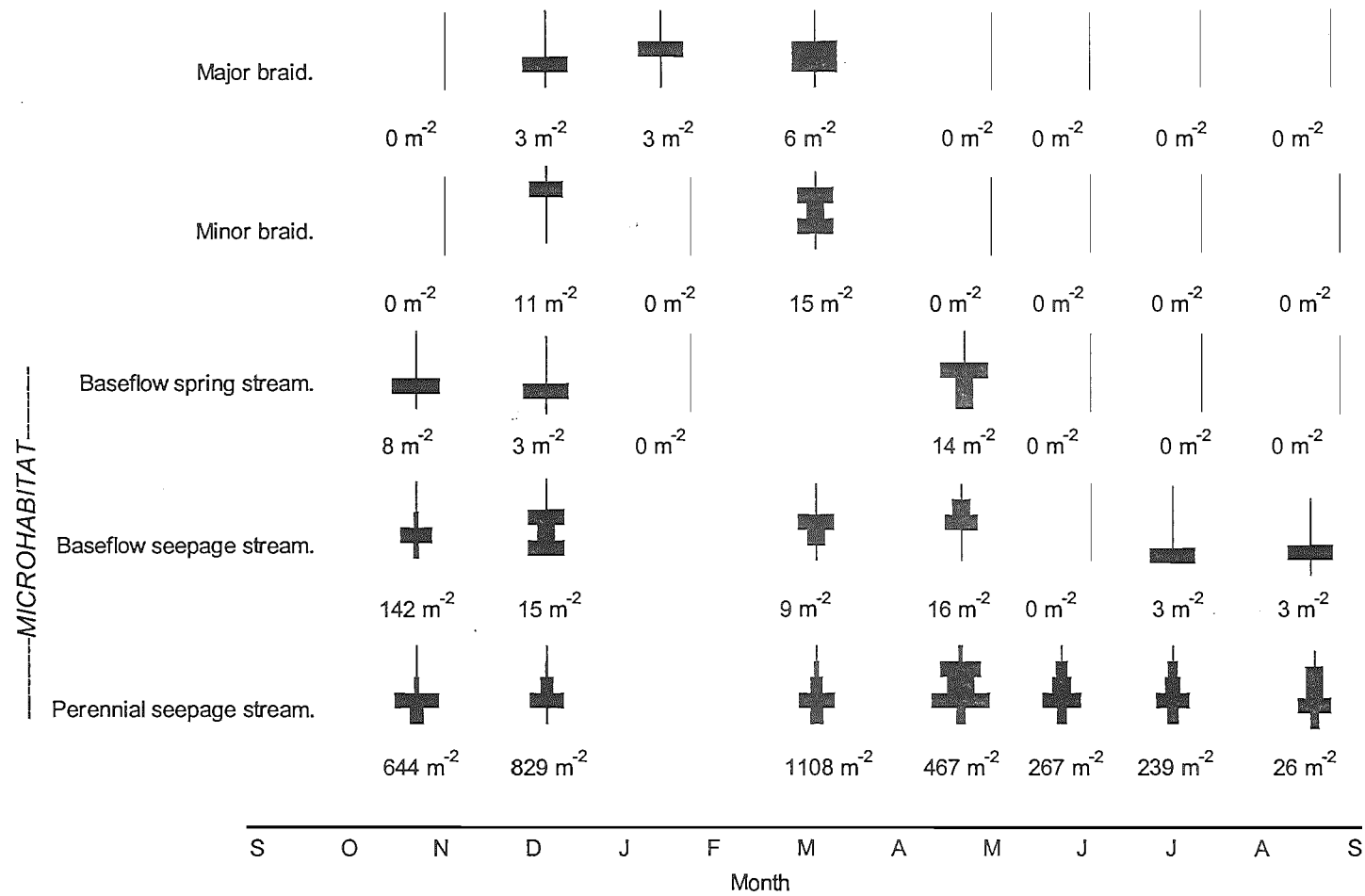


Figure 15. Size frequency distributions and mean densities of Elmidæ in the five habitats over the study period. In each graph, the bars from the bottom to the top represent the size classes: 0 - 2 mm; 2 - 4 mm; 4 - 6 mm; 6 - 8 mm; 8 - 10 mm (the scale of the bars varies between graphs).

## Production of Hydrobiosidae

*Hydrobiosis frater*, *H. parumbripennis*, and *H. umbripennis* were present, with the latter being most common. Hydrobiosidae contributed to total production at the two seepage streams only. Production estimates were 0.4 g DW m<sup>2</sup> yr<sup>-1</sup> in the perennial seepage stream and 0.1 g DW m<sup>2</sup> yr<sup>-1</sup> in the baseflow seepage stream (Table 5). Densities ranged from 115 m<sup>-2</sup> - 340 m<sup>-2</sup> in the perennial seepage stream, and from 15 - 292 m<sup>-2</sup> in the baseflow seepage stream (Figure 12). The production to biomass rate was approximately 5 in the perennial seepage stream (Table 5). The Hydrobiosidae appeared to have rapid growth from October to December, but it was difficult to trace the overlapping cohorts during winter and it was assumed that these 3 taxa of *Hydrobiosis* were univoltine with a CPI of 335 days.

## Production of *Pycnocentroides aureola*

The conoesucid caddisfly *Pycnocentroides aureola* was confined largely to seepage streams where production was estimated to be 0.7 g DW m<sup>-2</sup> yr<sup>-1</sup> (perennial seepage stream), and 0.1 g DW m<sup>-2</sup> yr<sup>-1</sup> (baseflow seepage stream) (Table 5). Larval densities ranged from 41 m<sup>-2</sup> to 781 m<sup>-2</sup>; and from 0 m<sup>-2</sup> to 137 m<sup>-2</sup>, respectively (Figure 13). The production to biomass rate was 4 (Table 5). *Pycnocentroides aureola* was assumed to be univoltine, but its life history information was too fragmented to interpret (Figure 13).

### Production of Zelandobius furcillatus

The stonefly Zelandobius furcillatus had a patchy distribution and few larvae were present from December 1997 to March 1998. A cohort with early instar larvae occurring in March, and mature larvae in August, when emerging adults were observed, can be seen in Figure 14. Production of Zelandobius furcillatus was approximately  $0.2 \text{ g DW m}^{-2} \text{ yr}^{-1}$  in the perennial seepage stream, and  $0.1 \text{ g DW m}^{-2} \text{ yr}^{-1}$  in the baseflow spring stream (Table 5). Larval densities ranged from 0 -  $330 \text{ m}^{-2}$  in the perennial seepage stream,  $0 \text{ m}^{-2}$  -  $161 \text{ m}^{-2}$  in the baseflow seepage stream, and from 0 -  $164 \text{ m}^{-2}$  in the baseflow spring stream (Figure 14). Production to biomass ratios ranged from 7 to 11 in the three streams but were not significantly different. The life history was however, reasonably well defined: larvae recruited in February were mature by mid August, and the CPI of 210 days was based on this. This life history pattern differs from that described by Winterbourn (1978) in a high country stream where juvenile larvae were present in spring and gradually matured to late instar larvae and adults in the winter of the following year.

### Production of Elmidae

The family Elmidae was represented by a single species that was not identified, but is probably a species of Hydora. Estimated production of Elmidae was  $0.8 \text{ g DW m}^{-2} \text{ yr}^{-1}$  in the perennial seepage stream (Table 5) and densities ranged from 26 -  $1108 \text{ m}^{-2}$ . Late instar larvae were most

abundant in April 1998 (Figure 15). The production to biomass rate was 6 (Table 5). There were several overlapping cohorts present, which made the life history information difficult to interpret. Nevertheless, this taxon was assumed to be univoltine, with a CPI of 335 days.

## Discussion

### Comparison between the Ashley, Waimakariri, and Rakaia Rivers

The Ashley, Waimakariri and Rakaia are all braided shingle bed rivers that flow east across the Canterbury Plains. The Ashley has its headwaters in the foothills and has a mean flow of  $15 \text{ m}^3\text{s}^{-1}$  (Scrimgeour *et al.*, 1989) whereas the Waimakariri and Rakaia both originate at high elevations near the main divide and have mean flows of about  $100 \text{ m}^3\text{s}^{-1}$  and  $200 \text{ m}^3\text{s}^{-1}$ , respectively (Hughey *et al.*, 1989). The greater production of benthic invertebrates in seepage channels relative to other channel types is apparent in both the foothills and alpine catchment rivers (Tables 4,5,6). *Deleatidium* production in the braids of the Ashley River, calculated from Hughey *et al.* (1989) was comparable to that calculated by Scrimgeour (1987). However, production of *Aoteapsyche* in braids of the Ashley ( $0.1$  to  $0.2 \text{ g DW m}^{-2} \text{ yr}^{-1}$ ) was much lower than that for *Aoteapsyche colonica* ( $3.13 \text{ g DW m}^{-2} \text{ yr}^{-1}$ ) recorded by Scrimgeour

(1991). Production varied across all three rivers and was greatest in the seepage streams.

Table 6. Estimated secondary production in different habitat types of (a) the Ashley River and (b) the Waimakariri River based on average dry weights, (g DW m<sup>-2</sup> yr<sup>-1</sup>), September 1985 to August 1986 supplied by Hughey *et al.* (1989), less common taxa are excluded.

(a) Ashley River

Braids	Major (> 1 m <sup>3</sup> s <sup>-1</sup> )	Minor (< 1 m <sup>3</sup> s <sup>-1</sup> )	Seepage (<< 1 m <sup>3</sup> s <sup>-1</sup> )
<i>Deleatidium</i> spp.	3.9	4.2	5.6
Chironomidae	0.1	0.1	0.2
Gripopterygidae	0.0	0.0	0.0
Rhyacophilidae	0.1	0.1	0.2
Hydropsychidae	0.1	0.2	0.2
Elmidae	0.3	0.7	2.2
Total	4.4	5.3	8.3

(b) Waimakariri River

Braids	Major (> 5 m <sup>3</sup> s <sup>-1</sup> )	Minor (< 5 m <sup>3</sup> s <sup>-1</sup> )	Seepage (<< 1 m <sup>3</sup> s <sup>-1</sup> )
<i>Deleatidium</i> spp.	2	1.6	7.7
Chironomidae	0.1	0.1	0.4
Gripopterygidae	0.0	0.0	0.0
Rhyacophilidae	0.1	0.0	0.2
Hydropsychidae	0.0	0.0	0.0
Elmidae	0.0	0.0	0.0
Total	2.2	1.7	8.3

Production values for *Deleatidium* in the seepage streams were 5.6 g m<sup>-2</sup> yr<sup>-1</sup>, 7.7 g m<sup>-2</sup> yr<sup>-1</sup>, and 2.6 - 2.9 g m<sup>-2</sup> yr<sup>-1</sup> for the Ashley, Waimakariri, and Rakaia Rivers, respectively. Although densities of *Deleatidium* were much lower in the Rakaia perennial seepage stream, those of *Aoteapsyche* and Chironomidae were relatively, much higher. Consequently, while species composition changed, total production in the seepage streams was similar in the three rivers (Tables 2, 4a, 4b). Species composition of the seepage

channels sampled by Hughey *et al.* (1989) was most similar to that in the baseflow seepage streams sampled in the Rakaia.

In contrast to the seepage streams, total production in the braids was highest in the Ashley, intermediate in the Waimakariri (Table 6) and extremely low in the Rakaia but note the variation in the size of the braids sampled (Table 3). Estimates of Deleatidium production derived from Hughey *et al.* (1989) were  $3.9 - 4.2 \text{ g m}^{-2} \text{ yr}^{-1}$  for braids in the Ashley. In the Waimakariri, Deleatidium production in the braids was about half that; i.e.,  $1.6 - 2 \text{ g m}^{-2} \text{ yr}^{-1}$ . Production in braids of the Rakaia was extremely low by comparison at  $0.3 - 0.4 \text{ g m}^{-2} \text{ yr}^{-1}$ .

Previous production estimates for South Island populations of Deleatidium range from 0.2 to  $4.5 \text{ g DW m}^{-2} \text{ yr}^{-1}$ . The highest of these values was obtained from a braided gravel river (Winterbourn, 1995). In these rivers Deleatidium are numerically dominant and can comprise 31 to 96% of the macroinvertebrate fauna in any one month (Pierce, 1983; Sagar, 1986; Scrimgeour, 1987; Scrimgeour & Winterbourn, 1989). Deleatidium production varies seasonally both within, and between, the foothills and alpine braided rivers, largely as a result of their hydrologic regimes (Pierce, 1979; Sagar, 1986; Scrimgeour, 1987).

In the middle - lower reaches of the Selwyn, a relatively stable - discharge gravel bed river originating in the foothills, Winterbourn (1973) calculated that  $3.5 \text{ g m}^{-2}$  of the total  $4.2 \text{ g m}^{-2} \text{ yr}^{-1}$  was contributed by

numerous overlapping cohorts developing rapidly over the summer months. In contrast, Scrimgeour (1987) calculated that  $3.6 \text{ g m}^{-2}$  of the total  $4.5 \text{ g m}^{-2} \text{ yr}^{-1}$ , had occurred over winter in braids of the Ashley River. This pattern was strongly influenced by flooding, particularly during spring and summer. The presence of greater biomass of invertebrates in winter is, however, typical of alpine - fed braided rivers such as the Rakaia and Cass (Sagar, 1986; Pierce, 1983). While flooding of alpine - fed rivers can occur in any month, discharges are generally lower and more stable from late summer, to spring, allowing a high invertebrate biomass to accrue. At the end of these seasonally stable - discharge periods, birds such as the wrybill begin breeding (Falla *et al.*, 1988; Pierce, 1983). Low summer production may not necessarily be characteristic of seepage microhabitats in these rivers, however. Thus Hughey *et al.* (1989) found that total dry weight of *Deleatidium* was much greater from late spring to autumn than at other times in seepage streams of the Waimakariri River where densities peaked at  $8500 \text{ ind. m}^{-2}$  and annual production was estimated to be  $7.7 \text{ g m}^{-2} \text{ yr}^{-1}$ . Furthermore, the dry weight of *Deleatidium* measured by Pierce (1979) in Rakaia microhabitats frequented by wrybill, indicated that production for the summer generation approached  $2.5 \text{ g m}^{-2}$ . While lower than either Winterbourn (1973) or Scrimgeour (1987) it is high for the Rakaia, since annual production was  $2.9 \text{ g m}^{-2} \text{ yr}^{-1}$  for the perennial seepage stream in my study.

The extremely low total production found in braids of the Rakaia in the present study is unlikely to be representative of production in braids

from year to year. Total production is likely to vary greatly between years because of variability in the flow regime between years, and therefore variability in the accrual of invertebrate biomass before it is limited by further flooding. Grzybkowska *et al.* (1996) reported an order of magnitude difference in annual production between two successive years in the Widawka River, Poland. This was a result of particularly severe flooding in their second year of study, and demonstrates that highly variable production can be expected in regions of variable and unpredictable precipitation. In the Rakaia River, Sagar (1986) recorded Deleatidium densities up to 5300 m<sup>-2</sup> in intermediate to large braids, values that are over an order of magnitude greater than densities obtained in this study. An El Nino Southern Oscillation increased the frequency and severity of flooding in the Rakaia River during my study (McKerchar & Unwin, 1998) as can be seen in Figure 16. These events also cause prolonged low flows in the Canterbury, foothills rivers. Scrimgeour (1987) noted that during his study there had been the longest period of stable flow in 13 years, spanning a 173 day spate free period. A similar spate free period last occurred on the Rakaia River in 1977. Production of Deleatidium in the braids of the Rakaia River may well have been similar to that recorded by Scrimgeour (1987) during this period in the absence of flood limitations on invertebrate biomass.

Deleatidium larvae are highly mobile animals that enter the drift frequently (Sagar & Glova, 1992). During floods, they have been found to congregate in refuge areas such as shallow river margins and pools



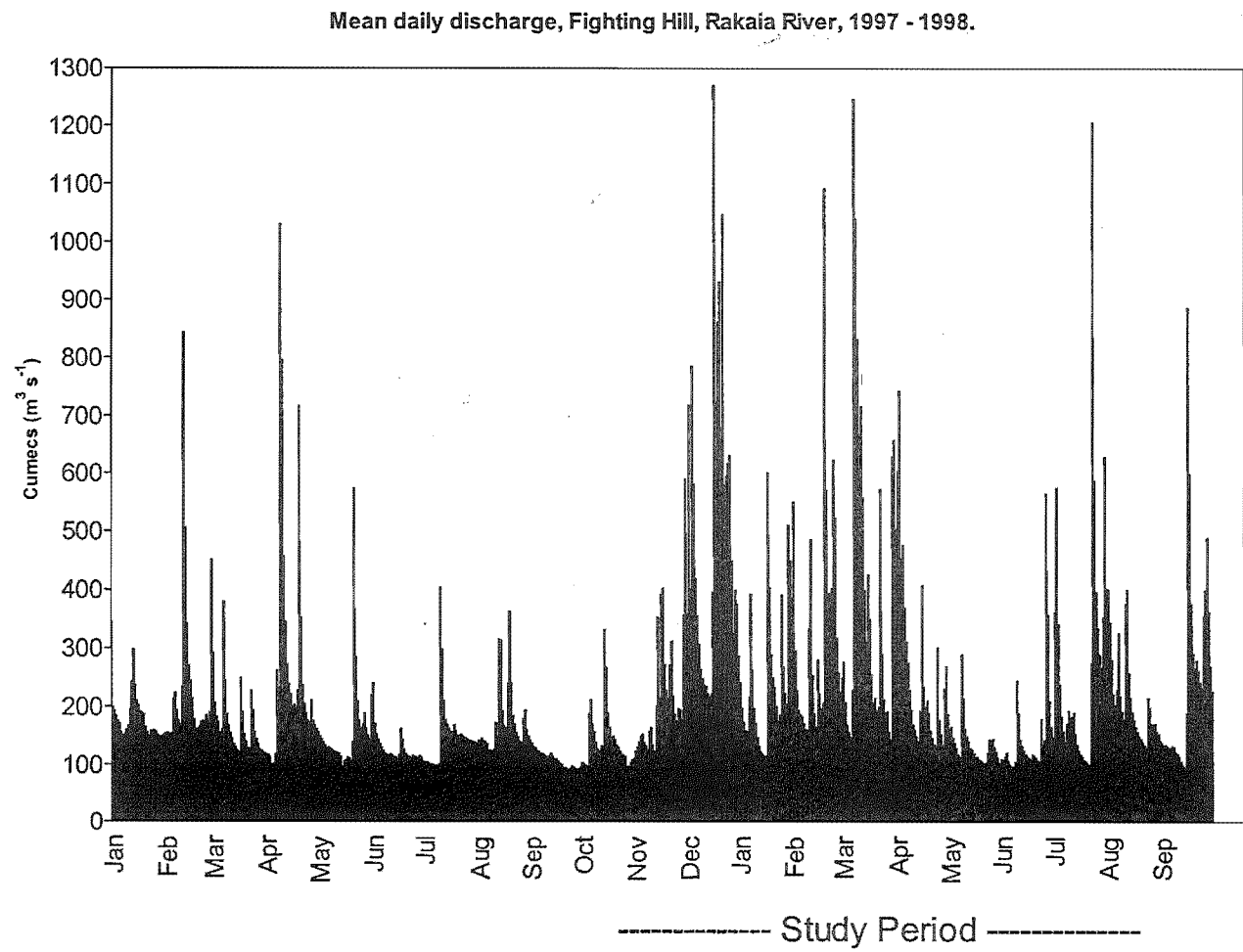


Figure 16. Discharge during the study period, and unseasonal flooding as a result of ENSO.

(Pierce, 1979), and they may be absent or poorly represented in the drift during spates (McLay, 1968; Graesser, 1987). In the Rakaia, Pierce (1979) noted that floods caused temporary but spectacular declines in the numbers of Deleatidium in shallow water. During one flood, an average density of 2 m<sup>-2</sup> were recorded along one braid margin, but as the river subsided, densities of 200 - 775 m<sup>-2</sup> were recorded. While redistribution of Deleatidium larvae is apparent in smaller spates, larger floods can result in losses through catastrophic drift (Sagar, 1986). Drift is probably responsible for most immigration and emigration of Deleatidium larvae from seepage and spring streams during freshes.

With respect to spates, patchy disturbance across the river bed is probably an important factor explaining density differences between habitats. Sagar (1983b) compared monthly dry weights of total invertebrates between minor and major braids in the Rakaia and concluded that the higher biomass in the former (1.344 g DW m<sup>-2</sup>, c.f. 0.539 g DW m<sup>-2</sup>) was a consequence of the more rapid recovery of invertebrate populations in minor braids, than major braids, as floods in the latter suppressed invertebrate numbers for longer periods. Data from Hughey *et al.* (1989) indicate that Deleatidium larval densities and mean individual DW within the various braids and seepage streams of the Waimakariri and Ashley Rivers, were most similar (and much reduced) after severe flooding. Early instar larvae dominated in the various habitats of both rivers after severe flooding, but smaller floods afterwards, often

suppressed recovery in the braids while seepage streams were often unaffected and maintained populations with a greater mean individual dry weight. In their study, the rate of accrual of total DW was often similar in the various channels during stable periods, however, particularly rapid increases in the density of early instar larvae were apparent in the seepage streams during such times, so overall, Deleatidium densities in the seepage streams were typically much higher than in the braids. These data of Hughey *et al.* (1989) also show that densities of Deleatidium increased rapidly during interflood periods in various habitats, but that the recovery was generally greatest within seepage streams.

There is some evidence that Chironomidae can "pick up the tab" when Deleatidium have been reduced in density following a succession of flood events. Chironomidae comprised a greater proportion of total production in the Rakaia than in the Waimakariri or Ashley Rivers. Their relatively high abundances meant that total invertebrate production within seepage streams was comparable in the Ashley, Waimakariri and Rakaia, despite differences in hydrologic regimes. I found that chironomids were generally associated with either thick growths of periphyton, or particulate organic matter, and brief periods of stable flow in the Rakaia, particularly after flooding in summer, resulted in a rapid growth of periphyton, and a rapid increase in the density of Chironomidae, possibly faster than that of Deleatidium. Chironomidae are likely to have much shorter generation times than Deleatidium, particularly in warmer waters. Mackey (1977) found CPIs ranging from 5 to 60 days for a diversity of British chironomid

species reared at 15 °C. Huryn (1998) estimated that one species of New Zealand Orthocladinae had a minimum cohort production interval of as little as 30 days in tributaries of the Taieri River.

In summary, data from the Waimakariri, Ashley, and Rakaia Rivers, suggest that differences in densities and dry weights of insects between seepage streams and braids, largely reflect varying rates of success of larvae likely recruited via oviposition and egg hatching rather than drift. Variation in flow - mediated disturbance across the river bed is clearly important. Poor survival of invertebrates in the more changeable conditions of the braids is evident, and differences in production between habitats appears to be primarily because braid populations are susceptible to more frequent flooding and associated scour than seepage streams.

Table 7. PRODUCTION OF *Deleatidium* spp., PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x6 (size groups)
0-2	407	0.005	1.9				
				8	0.015	0.1	0.7
2-4	400	0.026	10.4				
				291	0.122	35.5	213.0
4-6	109	0.218	23.8				
				-32	0.528	-16.7	0
6-8	141	0.838	117.9				
				116	1.309	151.9	911.2
8-10	25	1.780	43.9				
				23	2.538	57.6	345.5
10-12	2	3.295	6.4				
				2	3.295	6.4	38.6
			0.2 g m <sup>-2</sup>				1.9 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 1.93

$$\begin{aligned} \text{Annual Production} &= 1.93 \times 1.9 \\ &= 2.9 \text{ g DW m}^{-2} \text{ yr}^{-1} \end{aligned}$$

$$\text{Production / Biomass} = 14.3$$

Table 8. PRODUCTION OF *Deleatidium* spp., BASEFLOW SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x6 (size groups)
0-2	479	0.003	1.4				
				206	0.019	4.0	24.1
2-4	273	0.036	9.8				
				119	0.127	15.1	90.6
4-6	154	0.218	33.7				
				68	0.489	33.2	199.3
6-8	86	0.760	65.5				
				62	1.316	81.8	491.1
8-10	24	1.871	44.9				
				21	2.454	52.6	315.5
10-12	3	3.037	7.9				
				3	3.037	7.9	47.2
			0.2 g m <sup>-2</sup>				1.4 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 1.93

$$\begin{aligned} \text{Annual Production} &= 1.93 \times 1.4 \\ &= 2.3 \text{ g DW m}^{-2} \text{ yr}^{-1} \end{aligned}$$

$$\text{Production / Biomass} = 13.8$$

Table 9. PRODUCTION OF *Deleatidium* spp., BASEFLOW SPRING STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x6 (size groups)
0-2	290	0.003	0.8				
				122	0.016	2.0	11.8
2-4	168	0.030	5.0				
				126	0.116	14.7	88.2
4-6	42	0.203	8.5				
				20	0.463	9.4	56.3
6-8	22	0.723	15.7				
				17	1.341	22.4	134.6
8-10	5	1.958	9.8				
				2	2.819	5.3	31.8
10-12	3	3.680	11.6				
				3	3.680	11.6	69.5
			0.1 g m <sup>-2</sup>				0.4 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 1.93

Annual Production = 1.93 x 0.4  
= 0.8 g DW m<sup>-2</sup> yr<sup>-1</sup>

Production / Biomass = 14.7

Table 10. PRODUCTION OF *Deleatidium* spp., MINOR BRAID (< 10 m<sup>3</sup>s<sup>-1</sup>)

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (g m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x6 (size groups)
0-2	55	0.005	0.3				
2-4	86	0.027	2.3	-31	0.016	-0.5	0
4-6	15	0.211	3.2	71	0.119	8.4	50.7
6-8	13	0.723	9.5	2	0.467	0.8	5.1
8-10	3	1.746	4.7	10	1.235	12.9	77.6
10-12	0	3.242	1.2	2	2.494	5.7	34.3
				0	3.242	1.2	7.3
			0.0 g m <sup>-2</sup>				0.2 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 1.93

Annual Production = 1.93 x 0.2  
= 0.3 g DW m<sup>-2</sup> yr<sup>-1</sup>

Production / Biomass = 16



Table 11. PRODUCTION OF *Deleatidium* spp., MAJOR BRAID (> 40 m<sup>3</sup>s<sup>-1</sup>)

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x6 (size groups)
0-2	22	0.005	0.1	-18	0.021	-0.4	0
2-4	40	0.038	1.5	24	0.145	3.4	20.5
4-6	16	0.251	4.1	0	0.515	0.2	1.1
6-8	16	0.779	12.5	1	1.315	14.2	85.0
8-10	5	1.850	9.8	5	2.546	12.6	75.7
10-12	0	3.242	1.1	0	3.242	1.1	6.8
			0.0 g m <sup>-2</sup>				0.2 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 1.93

Annual Production = 1.93 x 0.2  
= 0.4 g DW m<sup>-2</sup> yr<sup>-1</sup>

Production / Biomass = 12.5

Table 12. PRODUCTION OF CHIRONOMIDAE, PERENNIAL SEEPAGE STREAM.

Size group (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x4 (size groups)
0 - 2	4363	0.006	27.7				
				2831	0.025	71.6	286.5
2 - 4	1532	0.044	67.8				
				1365	0.097	132.8	531.1
4 - 6	168	0.150	25.2				
				161	0.264	42.6	170.3
6 - 8	7	0.378	2.5				
				7	0.378	2.5	10
			0.1 g m <sup>-2</sup>				1.0 g m <sup>-2</sup>

Cohort Production Interval (CPI) = 137.5 days

Annual Production = (365/137.5) x 0.1  
= 2.6 g DW m<sup>-2</sup> yr<sup>-1</sup>

Production / Biomass = 21

Table 13. PRODUCTION OF CHIRONOMIDAE, BASEFLOW SEEPAGE STREAM.

Size group (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	$\Delta N$	Weight at loss, W (mg)	Weight lost W $\Delta N$	x4 (size groups)
0 - 2	1017	0.005	5.5				
				590	0.026	15.4	61.6
2 - 4	427	0.047	20.0				
				399	0.103	41.0	163.9
4 - 6	28	0.159	4.5				
				26	0.277	7.2	28.7
6 - 8	2	0.395	1.0				
				2	0.395	1.0	3.9
			0.0 g m <sup>-2</sup>				0.3 g m <sup>-2</sup>

Cohort Production Interval (CPI) = 137.5 days

$$\begin{aligned}\text{Annual Production} &= (365/137.5) \times 0.3 \\ &= 0.7 \text{ g DW m}^{-2} \text{ yr}^{-1}\end{aligned}$$

$$\text{Production / Biomass} = 22$$

Table 14. PRODUCTION OF CHIRONOMIDAE, BASEFLOW SPRING STREAM.

Size group (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	$\Delta N$	Weight at loss, W (mg)	Weight lost W $\Delta N$	x4 (size groups)
0 - 2	147	0.008	1.1				
				45	0.032	1.4	5.7
2 - 4	102	0.056	5.7				
				81	0.099	8.1	32.2
4 - 6	21	0.142	3				
				20	0.234	4.8	19.1
6 - 8	0	0.326	0.1				
				0	0.326	0.1	0.5
			0.0 g m <sup>-2</sup>				0.1 g m <sup>-2</sup>

Cohort Production Interval (CPI) = 137.5 days

$$\begin{aligned}\text{Annual Production} &= (365/137.5) \times 0.1 \\ &= 0.2 \text{ g DW m}^{-2} \text{ yr}^{-1}\end{aligned}$$

$$\text{Production / Biomass} = 15$$

Table 15. PRODUCTION OF CHIRONOMIDAE, MINOR BRAID (< 10 m<sup>3</sup>s<sup>-1</sup>).

Size group (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x4 (size groups)
0 - 2	41	0.005	0.2	-24	0.024	-0.6	0
2 - 4	65	0.043	2.8	56	0.107	5.9	23.8
4 - 6	10	1.71	1.6	9	0.275	2.5	10.2
6 - 8	0	0.378	0.1	0	0.378	0.1	0.5
			0.0 g m <sup>-2</sup>				0.0 g

Cohort Production Interval (CPI) = 137.5 days

Annual Production = (365/137.5) x 0.0  
= 0.1 g DW m<sup>-2</sup> yr<sup>-1</sup>

Production / Biomass = 19

Table 16. PRODUCTION OF CHIRONOMIDAE, MAJOR BRAID ( $> 40 \text{ m}^3 \text{s}^{-1}$ ).

Size group (mm)	Mean density (No. $\text{m}^{-2}$ )	Dry weight (mg)	Biomass ( $\text{mg m}^{-2}$ )	$\Delta \text{N}$	Weight at loss, W (mg)	Weight lost $W\Delta \text{N}$	x4 (size groups)
0 - 2	89	0.008	0.7				
2 - 4	175	0.056	9.7	-87	0.032	-2.8	0
4 - 6	14	0.176	2.5	161	0.116	18.7	74.7
6 - 8	1	0.365	0.2	13	0.270	3.6	14.4
				1	0.365	0.2	1
			<u>0.0 g <math>\text{m}^{-2}</math></u>				<u>0.1 g <math>\text{m}^{-2}</math></u>

Cohort Production Interval (CPI) = 137.5 days

$$\begin{aligned} \text{Annual Production} &= (365/137.5) \times 0.1 \\ &= 0.2 \text{ g DW m}^{-2} \text{ yr}^{-1} \end{aligned}$$

$$\text{Production / Biomass} = 18$$

Table 17. PRODUCTION OF *Aoteapsyche* spp., PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x5 (size groups)
0-4	150	0.050	7.6				
				89	0.199	17.7	88.5
4-8	61	0.347	21.3				
				40	1.474	59.6	298.0
8-12	21	2.601	54.6				
				-11	4.787	-53.0	
12-16	32	6.972	223.5				
				13	10.379	139.7	698.7
16-20	19	13.785	256.3				
				19	13.785	256.3	1281.7
			0.6 g m <sup>-2</sup>				2.4 g m <sup>-2</sup>

Cohort Production Interval correction = 365/335

Annual Production

= (365/335)\*2.4

= 2.1 g DW m<sup>2</sup> yr<sup>-1</sup>

Production / Biomass

= 4.6

Table 18. PRODUCTION OF ELMIDAE, PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x5 (size groups)
0-2	75	0.012	0.9				
				-281	0.028	-7.8	
2-4	356	0.044	15.7				
				230	0.168	38.8	193.7
4-6	126	0.293	36.9				
				70	0.596	41.8	209.4
6-8	56	0.899	50.2				
				49	1.160	57.2	285.8
8-10	7	1.421	9.3				
				7	1.421	9.4	46.7
			0.1 g m <sup>-2</sup>				0.7 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365/335

Annual Production

= (365/335)\*0.7

= 0.8 g DW m<sup>2</sup> yr<sup>-1</sup>

Production / Biomass

= 8



Table 19. PRODUCTION OF HYDROBIOSIDAE, PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x5 (size groups)
0-4	98	0.038	3.7				
				37	0.126	4.7	23.5
4-8	61	0.213	12.9				
				37	0.522	19.5	97.4
8-12	23	0.832	19.5				
				9	1.347	12.8	63.9
12-16	14	1.863	25.9				
				12	2.229	27.4	137.2
16-20	2	2.734	5.4				
				2	2.734	5.4	27.0
			0.1 g m <sup>-2</sup>				0.3 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365/335

$$\begin{aligned} \text{Annual Production} &= (365/335) \times 0.3 \\ &= 0.4 \text{ g DW m}^2 \text{ yr}^{-1} \end{aligned}$$

$$\text{Production / Biomass} = 4$$

Table 20. PRODUCTION OF HYDROBIOSIDAE, BASEFLOW SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	$\Delta N$	Weight at loss, W (mg)	Weight lost W $\Delta N$	x5 (size groups)
0-4	30	0.031	0.9				
				8	0.132	1.0	5.0
4-8	22	0.232	5.1				
				17	0.571	9.9	49.5
8-12	5	0.911	4.4				
				3	1.244	3.6	17.8
12-16	2	1.576	3.1				
				2	2.328	3.7	18.5
16-20	0	3.079	1.1				
				0	3.079	1.1	5.7
			0.1 g m <sup>-2</sup>				0.1 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365/335

$$\begin{aligned}\text{Annual Production} &= (365/335) \times 0.1 \\ &= 0.1 \text{ g DW m}^2 \text{ yr}^{-1}\end{aligned}$$

$$\text{Production / Biomass} = 7$$

Table 21. PRODUCTION OF *Pycnocentroides aureola*, PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x 6 (size groups)
0-2	62	0.021	1.3				
2-4	111	0.101	11.1	-48	0.061	-2.9	
4-6	50	0.339	17.0	60	0.220	13.3	79.7
6-8	58	1.032	60.1	-8	0.686	-5.5	
8-10	17	1.717	28.5	42	1.375	57.1	342.8
10-12	13	2.684	34.5	4	2.200	8.2	49.4
				13	2.684	34.5	207.1
			0.2 g m <sup>-2</sup>				0.7 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365/335

Annual Production = (365/335) x 0.7  
= 0.7 g DW m<sup>2</sup> yr<sup>-1</sup>

Production / Biomass = 4.8

Table 22. PRODUCTION OF *Pycnocentroides aureola*, BASEFLOW SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	$\Delta N$	Weight at loss, W (mg)	Weight lost W $\Delta N$	x 6 (size groups)
0-2	14	0.023	0.3				
				-11	0.062	-0.7	
2-4	26	0.101	2.6				
				21	0.244	5.1	30.4
4-6	5	0.388	1.9				
				-1	0.710	-0.5	
6-8	6	1.032	5.8				
				5	1.338	6.3	37.9
8-10	1	1.644	1.4				
				-1	2.419	-2.2	
10-12	2	3.194	5.5				
				2	3.194	5.5	33.3
			0.0 g m <sup>-2</sup>				0.1 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365 / 335

$$\begin{aligned} \text{Annual Production} &= (365/335) \times 0.1 \\ &= 0.1 \text{ g DW m}^2 \text{ yr}^{-1} \end{aligned}$$

$$\text{Production / Biomass} = 6$$

Table 23. PRODUCTION OF *Zelandobius furcillatus*, PERENNIAL SEEPAGE STREAM

Size group length (mm)	Mean density (No. m <sup>-2</sup> )	Dry weight (mg)	Biomass (mg m <sup>-2</sup> )	ΔN	Weight at loss, W (mg)	Weight lost WΔN	x 4 (size groups)
0-2	17	0.035	0.6				
				-47	0.095	-4.5	
2-4	64	0.155	9.9				
				50	0.331	16.7	66.8
4-6	14	0.507	6.9				
				10	0.916	9.6	38.3
6-8	3	1.324	4.1				
				3	1.324	4.1	16.3
			0.0 g m <sup>-2</sup>				0.1 g m <sup>-2</sup>

Cohort Production Interval (CPI) correction = 365/210

Annual Production = (365/210) x 0.1  
= 0.2 g DW m<sup>2</sup> yr<sup>-1</sup>

Production / Biomass = 10

## CHAPTER 4

# QUALITY OF HABITAT

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### Introduction

Variation in flow - mediated disturbance across the river bed is clearly important in the larger braided rivers in the South Island such as the Waimakariri and Rakaia by limiting invertebrate numbers in the braids. Contributing factors that may also help to explain the high production in the seepage streams are: food quality and quantity, temperature, and habitat complexity. Such factors are also likely to be indirectly influenced by the discharge regime, and ever changing nature of the habitats.

In this chapter, contributing factors which may cause higher production in the seepage microhabitats are discussed. Sites are first described on the basis of the gradients that separate them. Most of the gradients measured probably carry information about the disturbance history of each site in the period immediately prior to sampling. Fine particulate organic matter and algal abundance were measured to identify patchiness in food resources among habitats. However, algal abundance could also be interpreted as a measure of biomass accrual in the absence of scour. A positive, vertical hydraulic gradient implies isolation from the braids, varying shelter from small freshes, and also absence of glacial flour from the water column during baseflow. During floods, braids are

swifter and more frequently subjected to scour and fill events, and therefore tend to have less interstitial silt. Quieter reaches with unscoured beds tend to accumulate silt. Other physical gradients that were measured included temperature, oxygen, and substrate composition.

## **Methods**

The following variables were collected in conjunction with each invertebrate sample: vertical hydraulic gradient, water temperature, algal abundance, dissolved oxygen, conductivity, and substrate size. Vertical hydraulic gradient data was collected by temporarily installing a manometer (after Boulton, 1993) over a standpipe inserted to 400 mm. Vertical hydraulic gradient is a unitless measure, positive values, typically indicating upwelling, and negative values, downwelling. Most readings were taken after about 5 - 10 minutes, although constant readings were often reached within a few seconds of installing the manometer since some localities were very porous. Spot water temperatures were measured at the time of sampling, both at the surface and in the standpipe.

Algal abundance was assessed visually as described by Jowett & Richardson (1990): 1, stones clean and surface rough; 2, stones slippery but no growths visible; 3, thin algal growths visible; 4, algae abundant; 5, thick covering of algae over 80% of upper stone surfaces. Fine particulate

organic matter (FPOM) and coarse particulate organic matter (CPOM) were collected along with the invertebrate samples (mesh 0.1 - 0.3 mm). CPOM included material retained by a 1mm sieve and FPOM included material between 1 mm and 0.1 mm. Detrital fractions were dried at 70 °C for at least 5 days and kept in a desiccator before weighing and ashing at 550 °C for 12 hours. Ashed samples were then kept in a desiccator until weighing ( $\pm 0.005$  g).

In the laboratory, dissolved oxygen (YSI model 57 oxygen meter) and conductivity (HI 8333 meter) were measured from one litre water samples collected from the surface and the standpipe. In the field, care was taken to gently pour the interstitial water along the sides of the glass jars which were then sealed after checking that no air bubbles were present. All measurements of dissolved oxygen and conductivity (at 25 °C) were taken 2 - 7 hours after their collection.

Surface substrate size was assessed visually for each quadrat prior to sampling using the following size classes: sand (< 2 mm); small gravel (2 - 32 mm); large gravel (32 - 64 mm); small cobbles (64 - 128 mm); large cobbles (128 - 256 mm); and boulders (256 - 330 mm). Core samples were collected beside each quadrat to estimate sub - surface bed composition after invertebrate samples had been obtained. The cores were taken with a 100 mm internal diameter stainless steel cylinder to a depth of approximately 100 mm. When the bed was well armoured a



pivoting rotation was used to both loosen the bed and drive the core down between larger cobbles and boulders. Once in place, the corer was tilted while still in the bed and one hand was worked into the bed to cup the bottom of the corer for removal. Silt ( $< 63 \mu$ ) was collected by repeatedly recycling 1 litre of water during wet sieving, and finally rinsing each size class to minimise the amount of wash water. Silt was allowed to settle for two - three weeks, after which excess water was carefully siphoned off and the silt dried and weighed ( $\pm 0.005$  g). Substrate composition of cores was then determined by passing dry sediments through sieves with pore sizes of 32 mm, 16 mm, 8 mm, 4 mm, 2 mm, 1 mm, 500  $\mu$ m, 250  $\mu$ m, 125  $\mu$ m, and 63  $\mu$ m. Values for wash water silt and remaining dry sieved silt were combined. All data are contained in the Appendices.

## Statistics

Site data were aggregated, and where necessary, distributions of the variables were normalized by the transformations listed in Table 24 using the Statistix package. Pearson correlations were used to compare interrelationships between the variables, except that Spearman Ranks were used to compare inter-relationships with algal abundance. Multiple regression with a forward stepwise procedure was used to identify the variables most important in explaining variation in invertebrate dry weights and production across the river bed. Algal abundance could not be included in the stepwise regression as it was an ordinal variable. However,

it was considered that conductivity difference between surface water and the underlying interstices would partly represent it. A substrate index was calculated by the following formula  $(0.1 \times \% \text{ silt}) + (0.2 \times \% \text{ sand}) + (0.3 \times \% \text{ gravel}) + (0.4 \times \% \text{ cobble})$ . Relative production for each quadrat was estimated by calculating the dry weight of the various invertebrates and multiplying them by their respective production / biomass ratios.

Table 24. Variables and their transformations.

Variable	Units	Transformations
Total DW*P/B	g DW m <sup>-2</sup>	Log (x+1)
DW <i>Deleatidium</i>	g DW m <sup>-2</sup>	Log (x+1)
DW Chironomidae	g DW m <sup>-2</sup>	Log (x+1)
Total invertebrate density	ind m <sup>-2</sup>	Log (x+1)
Temperature (surface)	°C	
Temperature (400 mm depth)	°C	
Conductivity (surface)	µScm <sup>-1</sup>	Log
Conductivity (400 mm depth)	µScm <sup>-1</sup>	Log
Conductivity difference	µScm <sup>-1</sup>	Log
Dissolved Oxygen (surface)	mg O <sub>2</sub> L <sup>-1</sup>	
Dissolved Oxygen (400 mm depth)	ppm	
VHG	no unit	x+1
Periphyton	no unit	
CPOM	g m <sup>-2</sup>	Log (x+1)
FPOM	g m <sup>-2</sup>	Log (x+1)
Silt	g 0.1 m <sup>-3</sup>	Log (x+1)
% cobbles and gravels (bed)	proportion	arc sin√
% coarse sand (bed)	proportion	arc sin√
% fine sand (bed)	proportion	arc sin√
% cobbles (surface)	proportion	arc sin√
% gravels (surface)	proportion	arc sin√
Substrate index	proportion	

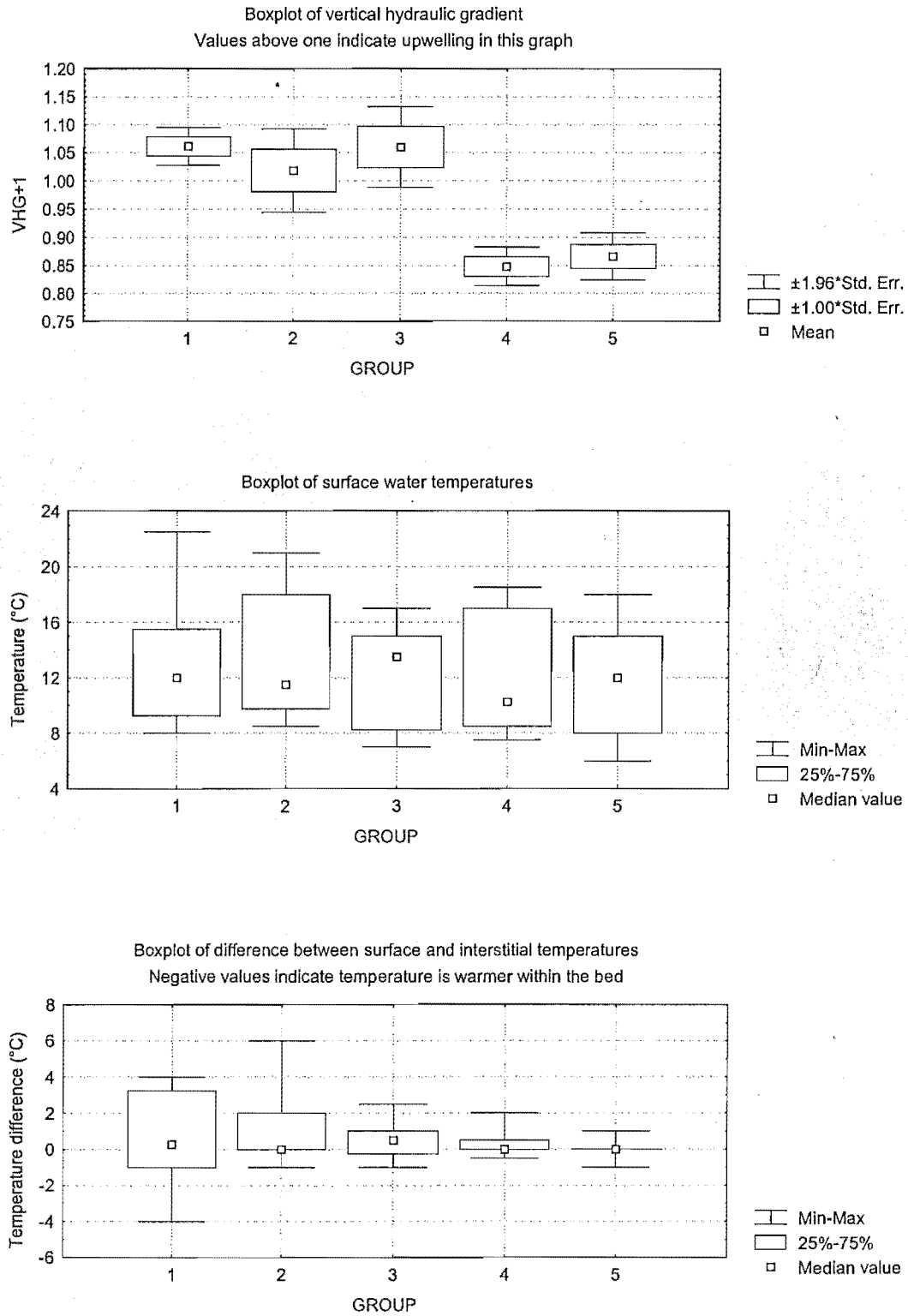


Figure 17. Vertical hydraulic gradient and temperature in the various channels. Groups are numbered as follows: 1, Perennial seepage stream; 2, Baseflow seepage stream; 3, Baseflow spring stream; 4, Minor braid; 5, Major braid

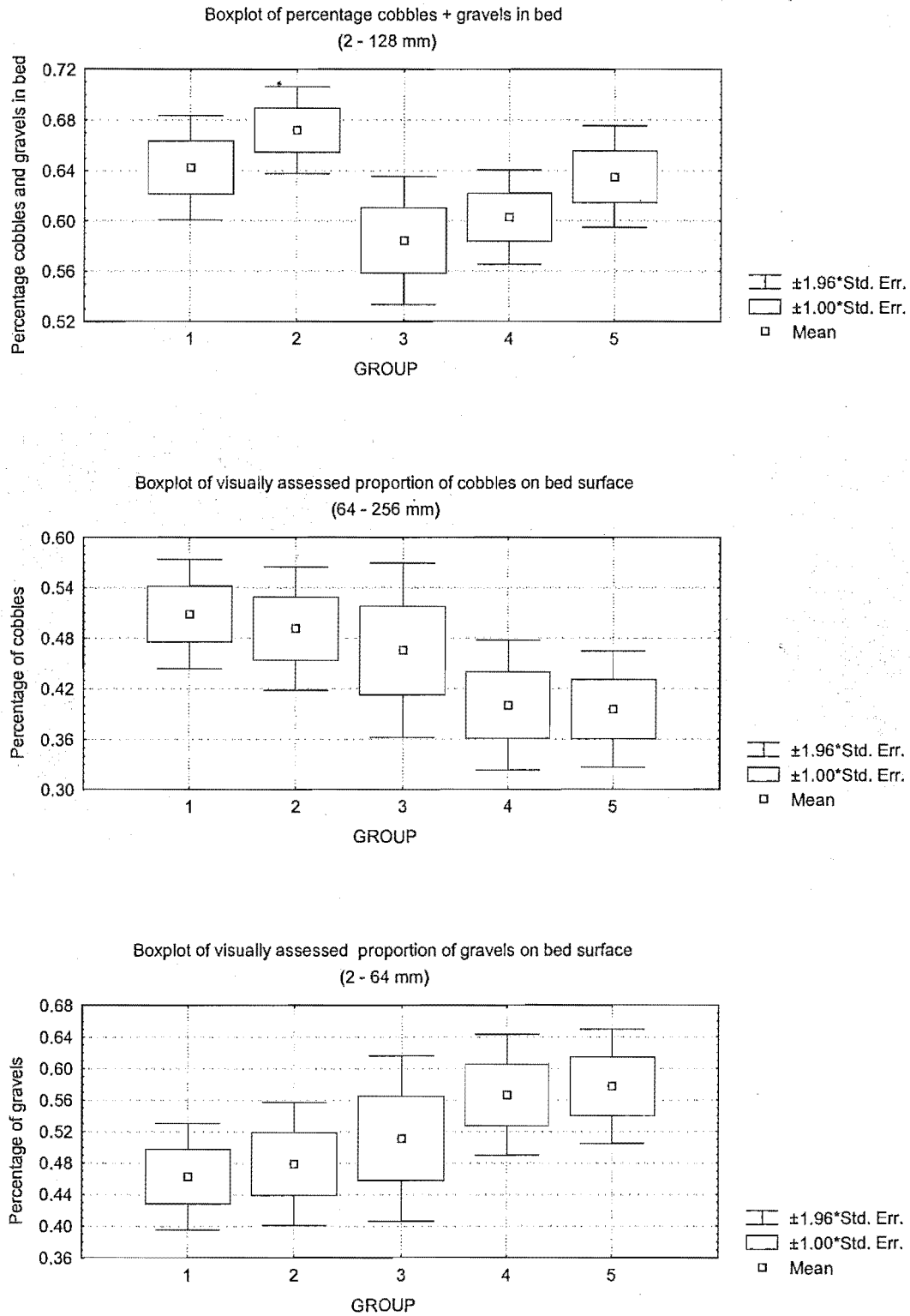


Figure 18. Bed composition in the various channels. Groups are numbered as follows: 1, Perennial seepage stream; 2, Baseflow seepage stream; 3, Baseflow spring stream; 4, Minor braid; 5, Major braid

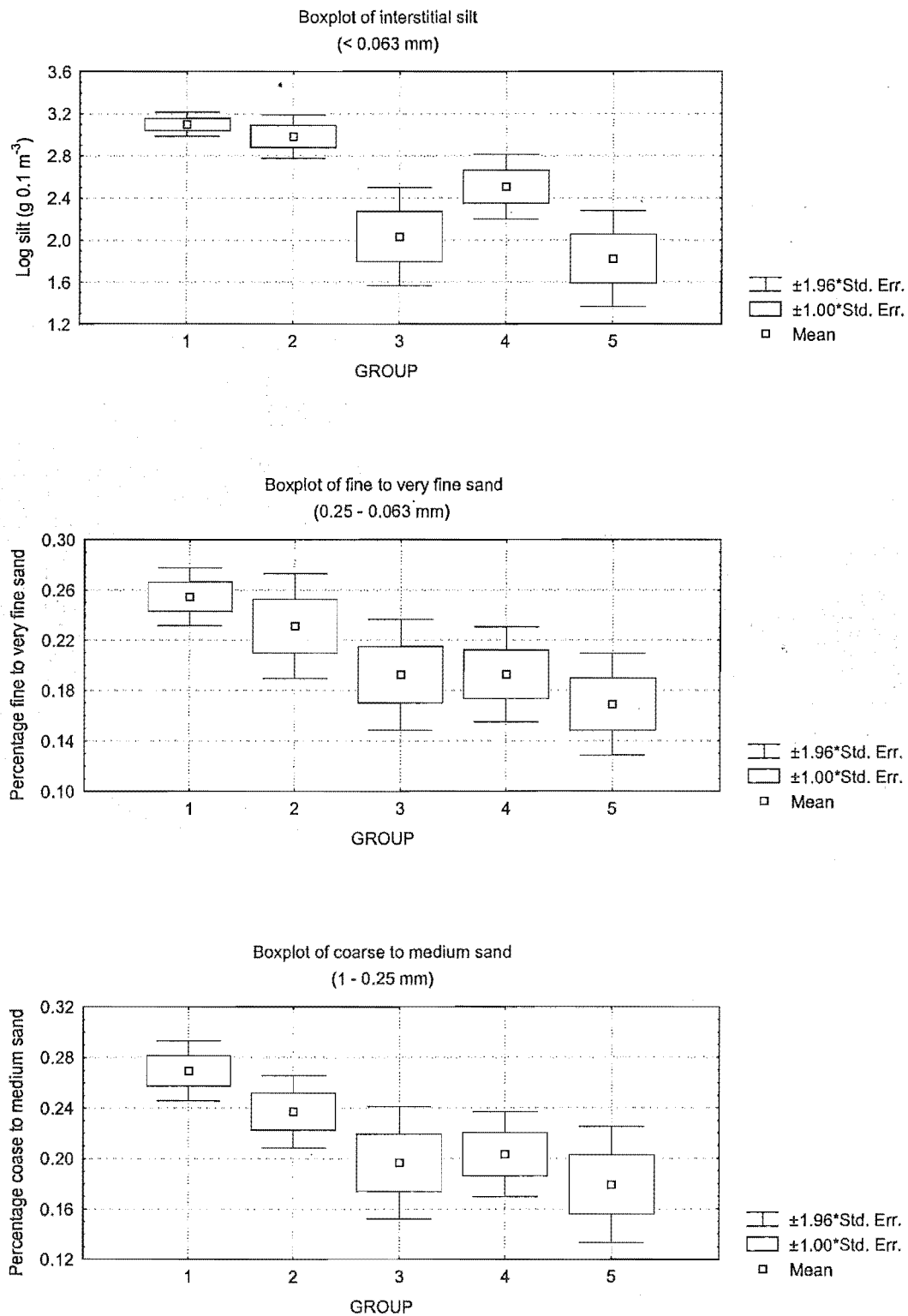


Figure 19. Accumulation of fines in the various channels. Groups are numbered as follows: 1, Perennial seepage stream; 2, Baseflow seepage stream; 3, Baseflow spring stream; 4, Minor braid; 5, Major braid

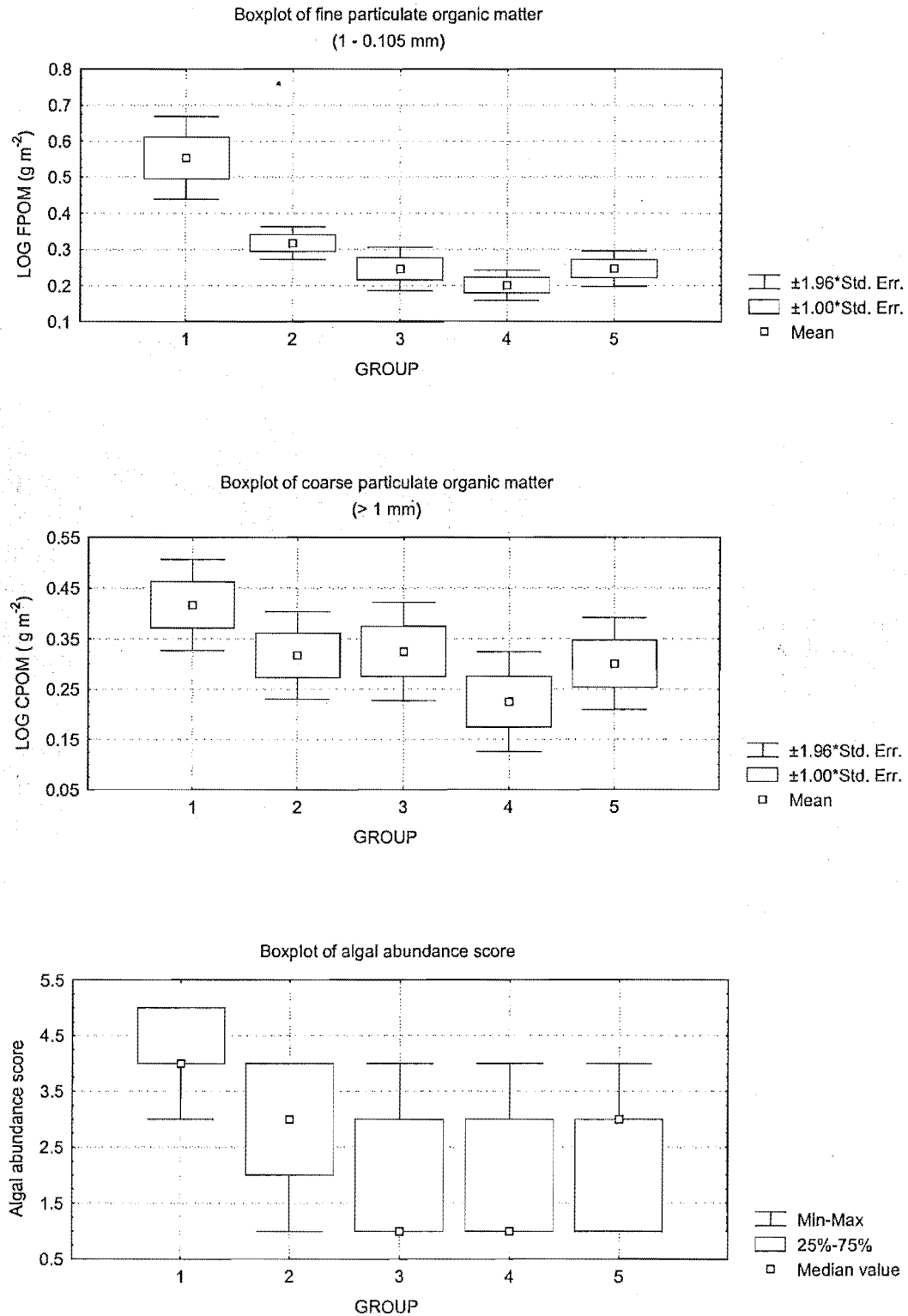


Figure 20. Accumulation of organic matter in the various channels. Groups are numbered as follows: 1, Perennial seepage stream; 2, Baseflow seepage stream; 3, Baseflow spring stream; 4, Minor braid; 5, Major braid

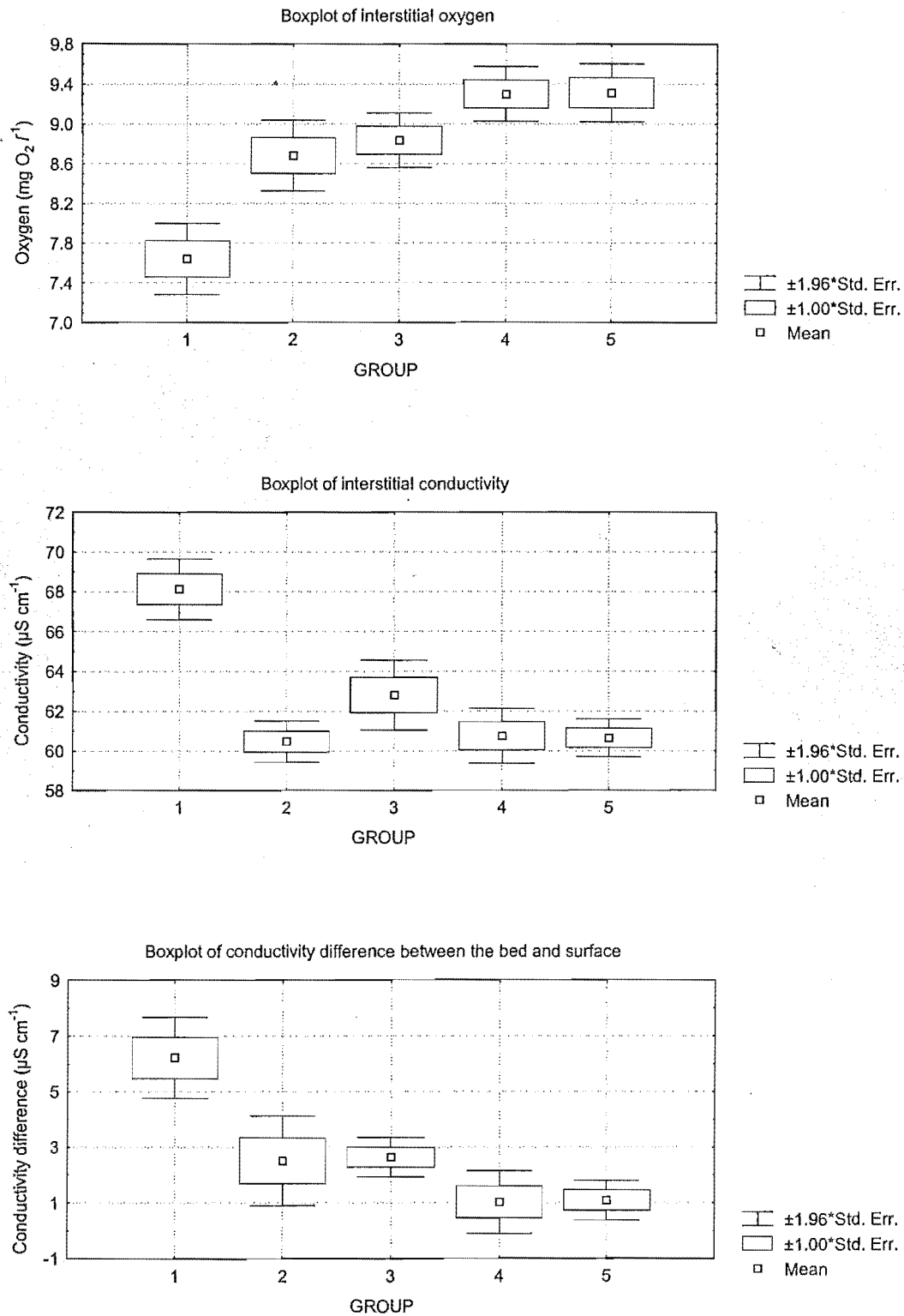


Figure 21. Oxygen and conductivity in the various channels. Groups are numbered as follows: 1, Perennial seepage stream; 2, Baseflow seepage stream; 3, Baseflow spring stream; 4, Minor braid; 5, Major braid

## Results

Seepage streams were generally upwelling throughout their reaches (Figure 17). The highest upwellings were found in spring streams, although in places of high porosity a nil or low VHG was sometimes obtained. The braids, in contrast, were moderately to strongly downwelling, with downwelling being high at the top of riffles, and greatest at the top of chute channels. The spring streams also tended to have less variable temperature regimes, moderated by their proximity to subsurface discharges (Figure 17). They tended to be markedly cooler than the seepage streams during summer afternoons (up to 5 - 8 °C). The highest temperature (22.5 °C) was recorded in a perennial stream which indicated that the diffuse seepages were unable to moderate summer heating as effectively as the spring streams as also found by Mosley (1983). On average, day time temperatures in seepage streams, were 1 - 2 °C warmer than the braids.

Visual assessment indicated that substrate composition was highly variable with little apparent difference between sites. However, on average, the fraction of gravels at the surface (2 - 64 mm) increased from the seepage streams to the braids whereas the fraction of cobbles (64 - 256 mm) decreased, and baseflow spring stream samples were most heterogeneous (Figure 18). This suggested that riffles in the perennial seepage streams may have been more armoured than those in the braids.



The proportion of smaller cobbles and gravels in the bed (2 - 128 mm) was similar between channels (Figure 18). Cobbles and gravels were generally packed together within coarse - fine sands and silt. Interstitial silt, was abundant in the seepage streams, and notably less common in the spring streams and braids (Figure 19). While much more variable, the percentage of sand also tended to be slightly less in the spring streams and braids. Therefore riffles in spring streams and major braids were generally more porous than other channels.

Fine particulate organic matter was sparsely distributed across the river bed of the Rakaia. In the braids FPOM ranged between 0.21 - 3.68 g m<sup>-2</sup>, but was most common in the seepage streams ranging between 0.35 - 34.1 g m<sup>-2</sup> (Figure 20). Coarse particulate organic matter followed a similar but much more variable trend (Figure 20). Algal abundance was assessed to be greatest in the perennial seepage stream throughout the year, and least in the braids (Figure 20). All habitats were generally well oxygenated both on the surface (range 7.9 - 10.6 mg O<sub>2</sub> L<sup>-1</sup>) and within the bed (5.5 - 10.4 mg O<sub>2</sub> L<sup>-1</sup>). However, interstitial oxygen was greatest in the braids, declined in the baseflow streams, and was least in the perennial seepage stream (Figure 21). In contrast, conductivity was highest in the perennial seepage stream both in the bed (62.7 - 80 µS cm<sup>-1</sup>) and at the surface (57.1 - 73.7 µS cm<sup>-1</sup>). Differences between bed and surface conductivity averaged 6 µS cm<sup>-1</sup> (Figure 21). Differences in conductivity, temperature, and dissolved oxygen between subsurface and

surface waters were least in the braids, and probably reflected both greater rates of infiltration, and the occurrence of less organic matter (and associated microorganisms) within the bed.

### **Interrelationships between variables**

Significant correlations between variables are shown in Table 25.

The weight of interstitial silt was significantly correlated with most aspects of bed composition (Table 25;  $P < 0.01$ ), but was most strongly correlated with the percentage of coarse - medium sand ( $r_p = .52$ ,  $P < 0.001$ ), this suggests silt particles were trapped via infiltration through the sand bed. The percentage of cobbles and gravels was weakly correlated with CPOM dry weight ( $r_p = .30$ ,  $P < 0.001$ ), which suggests there is a tendency for debris to accumulate either within gravels or around large cobbles and boulders.

Interstitial oxygen concentration was negatively correlated with vertical hydraulic gradient, conductivity, temperature, algal abundance, CPOM dry weight and FPOM dry weight ( $P < 0.01$ ; Table 25). Conductivity difference was weakly and positively correlated with VHG, FPOM dry weight, and algal abundance ( $P < 0.01$ ; Table 25), and negatively correlated with interstitial oxygen concentration ( $r_p = .52$ ,  $P < 0.001$ ), but was not correlated with weight of interstitial silt or temperature (Table 25). Therefore, high values of conductivity difference in association with low oxygen concentrations and high amounts of interstitial silt, probably

indicated a "long" residence time for subsurface water, and was likely influenced by the amount of algae, and FPOM, in the stream bed and on the surface.

### **Relationships between habitat variables and invertebrate distribution.**

Stepwise regression indicated that vertical hydraulic gradient was the best predictor of *Deleatidium* density. It explained 20% of the total variation, while conductivity difference (9%), interstitial silt dry weight (5%), and temperature (4%) explained a further 18% of the variation in the density of *Deleatidium* (Table 27). Similarly, vertical hydraulic gradient and interstitial silt dry weight explained 22% and 10%, respectively, of the variation in *Deleatidium* dry weight, while conductivity difference explained 8%, and FPOM dry weight 4% (Table 27). Vertical hydraulic gradient, and interstitial silt were considered to reflect a gradient of disturbance, and conductivity difference may have partly represented a gradient of declining interstitial water velocity and the gradual accumulation of organic matter in the absence of scour. *Deleatidium* density was biased towards early instar larvae at high densities. My observations indicate that early instar larvae were most commonly associated with pristine, upwelling water in recently scoured gravels that sometimes contained relatively high amounts of silt and sand within 5 - 10 cm of the surface. These sites also collected fine organic and inorganic particles. The inclusion of temperature in the stepwise regression indicated that densities varied seasonally (Table 27).

Deleatidium density and dry weight was only weakly associated with FPOM and algal abundance, although the former appeared to explain a slightly greater proportion (Table 26). Patchy disturbance within the river was partly represented by vertical hydraulic gradient which explained the single greatest proportion of variation, and by the occurrence of interstitial silt, these two variables explained the greatest portion of variation in both Deleatidium density and dry weight.

Algal abundance and densities of chironomid larvae were highly correlated (Table 26). Of the variables that were included in the stepwise regression, 34% of the variation in chironomid density could be accounted for (Table 27). FPOM explained 16%, conductivity difference 6%, followed by VHG (4%), interstitial silt (3%), and substrate (5%). Similarly, FPOM also explained 24% of the variation in chironomid dry weight, followed by conductivity difference (5%), interstitial silt (4%) and VHG (4%) (Table 27). Densities and dry weights of Chironomidae therefore largely reflected either algal standing crop, or accumulation of FPOM within the river bed.

Total invertebrate numbers were biased towards early instar chironomids at high densities, and almost half the variation could be explained (Table 27). FPOM explained the greatest proportion of the variation (27%), followed by conductivity difference (16%), silt (10%), and temperature (3%). Conductivity difference was the best predictor of total production, explaining 22% of the variation, followed by interstitial silt (16%), FPOM (10%), and temperature (3%). Perhaps not surprisingly, the

Table 25. Correlations between the variables defined in Table 24, Pearson correlations unless otherwise stated.

VARIABLE	VHG	TEMP	TEMP40	TEMPTDIFF	OXYGEN	CPOM	FPOM	ALGAE <sup>a</sup>	COND	COND40	CONDDIFF	SILT	%COBGRV	%FINESAND	%CMSAND	SUBSTRAT	V.%GRAV	V.%COB
TEMP	ns																	
TEMP40	ns	.9354**																
TEMPTDIFF	ns	.6286**	.3131**															
OXYGEN	(-).2946**	(-).4602**	(-).4201**	(-).3122**														
CPOM	ns	ns	ns	ns	(-).2631*													
FPOM	ns	ns	ns	ns	(-).3245**	.5297**												
ALGAE <sup>a</sup>	ns	.2355*	.2213**	ns	(-).4163**	ns	.5016**											
COND	ns	.3297**	.2416*	.3542**	(-).3680**	ns	ns	ns										
COND40	ns	.2590*	ns	.3188**	(-).6570**	.2516*	.3191**	.3643**	.6278**									
CONDDIFF	.2870*	ns	ns	ns	(-).5218**	ns	.2335*	.2556*	ns	.7355**								
SILT	.2256*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns							
%COBGRV	ns	ns	ns	ns	ns	.2995**	.2348*	ns	ns	ns	ns	.3129**						
%FINESAND	ns	ns	ns	ns	ns	ns	ns	.2419*	ns	ns	ns	.4217**	.2552*					
%CMSAND	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	.5154**	.2481*	.6573**				
SUBSTRAT	ns	ns	ns	ns	ns	.3333**	.2594*	ns	ns	ns	ns	.3654**	.9793*	.3580**	.3249**			
V.%GRAV	ns	(-).2220*	(-).2213*	ns	ns	ns	ns	ns	ns	ns	ns	(-).3242**	ns	(-).2696*	(-).2357*	ns		
V.%COB	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	(-).2714**	ns	ns	ns	ns	(-).9093**	
V.SUBSTRA	ns	.3164**	.3205**	ns	(-).2331*	ns	ns	ns	ns	ns	ns	.2768*	ns	.2732*	ns	ns	(-).8557**	.6935**

<sup>a</sup>Spearman Rank

\*, P&lt;0.01;\*\*P&lt;0.001

Table 26. Correlations between invertebrate densities, dry weight (DW), production, and measured habitat variables.  
Pearson correlations unless otherwise stated.

	Deleatidium DENSITY	<i>Deleatidium</i> DW	Chironomidae DENSITY	Chironomidae DW	Total DENSITY	PRODUCTION
Vertical hydraulic gradient	.3980**	.4130**	ns	ns	.2721*	.3025**
Surface water temperature	ns	ns	ns	ns	.2223*	ns
Interstitial water temperature	ns	ns	ns	ns	ns	ns
Temperature difference	.2227*	ns	ns	ns	.2468*	ns
Interstitial Oxygen	(-).3592**	(-).3631**	(-).2683*	(-).3354*	(-).5029**	(-).4177**
CPOM	ns	ns	ns	.2210*	ns	ns
FPOM	.2977**	.3552**	.4028**	.4977**	.5160**	.4697**
Algal abundance <sup>a</sup>	.2613*	.2352*	.7029**	.6586**	.6507**	.4555**
Surface water conductivity	ns	ns	ns	ns	ns	ns
Interstitial conductivity	.3600**	.2942**	.3428**	.3225**	.5165**	.4372**
Conductivity difference	.4359**	.4417**	.3533**	.3310**	.5312**	.4912**
Interstitial silt	.3598**	.4339**	ns	.3172**	.3613**	.4656**
%Cobbles gravels	ns	ns	ns	ns	ns	ns
%Fine sand	ns	.2461*	ns	ns	ns	.2202*
%Coarse - medium sand	.2297*	ns	ns	ns	ns	0.2697*
Substrate index	ns	.2348*	ns	ns	ns	ns
Visual %gravel	(-).2772*	ns	ns	ns	ns	(-).2264*
Visual %Cobble	.2765*	ns	ns	ns	ns	ns
Visual substrate index	.2224*	ns	ns	ns	ns	ns

<sup>a</sup>Spearman Rank

\*, P<0.01; \*\*, P<0.001

Table 27. Variables included in stepwise regression models predicting invertebrate density, dryweight, and production.  
 Probabilities:\*,P<0.01; \*\*, P<0.001, N=number of quadrats.

	N	% Variation explained	Cumulative % variation explained	F-value	P	Variables	T-value	P
<i>Deleatidium</i> density	140	20%	20%	20.31	**	Vertical hydraulic gradient	3.98	**
		9%	28%			Conductivity difference	3.39	**
		5%	33%			Interstitial silt	3.24	*
		4%	38%			Temperature	3.08	*
<i>Deleatidium</i> dry weight	140	22%	22%	25.7	**	Vertical hydraulic gradient	3.95	**
		10%	32%			Interstitial silt	4.19	**
		8%	39%			Conductivity difference	3.32	*
		4%	43%			FPOM	2.91	*
Chironomidae density	140	16%	16%	13.51	**	FPOM	5.13	**
		6%	22%			Conductivity difference	4.4	**
		4%	26%			Vertical hydraulic gradient	-3.51	**
		3%	29%			Interstitial silt	3.13	*
		5%	34%			Substrate index	-3.03	*
Chironomidae dry weight	140	24%	24%	20.29	**	FPOM	5.85	**
		5%	30%			Conductivity difference	3.73	**
		4%	33%			Interstitial silt	3.46	**
		4%	38%			Vertical hydraulic gradient	-3.03	*
Total invertebrate density	140	27%	27%	37.9	**	FPOM	6.65	**
		16%	42%			Conductivity difference	5.97	**
		5%	47%			Interstitial silt	4.73	**
		6%	53%			Temperature	3.77	**
Production	140	22%	22%	34.41	**	Conductivity difference	5.35	**
		16%	38%			Interstitial silt	5.86	**
		10%	48%			FPOM	5.11	**
		3%	50%			Temperature	2.71	*

data indicated that total invertebrate density and production were associated with less frequently scoured habitats thus, density and production increased along a gradient of increasing interstitial silt, retention of subsurface water, that had on the average, a greater quantity of algae and FPOM.

## Discussion

Frequent floods act to structure the food quantity and quality within river beds, by influencing the availability of particulate organic matter, and by affecting algal production. Winterbourn *et al.* (1984) studied food resources and ingestion patterns of benthic insect larvae in the Inangahua River, West Coast, using gut content and stable carbon isotope analyses. They found  $^{13}\text{C} / ^{12}\text{C}$  ratios of insects in the main river were similar to those in the forested tributaries and indicated allochthonous dependence by the fauna. Because bed materials were continually shifting and being abraded by saltating fine sediments, algal populations appeared to have little opportunity to become established and consequently their availability as food for insects was limited. They concluded that fragments of wood and fine particulate material scavenged by floodwater from the catchment and extensive shingle bed, were redistributed within the river channels, and provided the basis for insect production.



In braided rivers, algae remains an important food source for collector browsers for much of the year despite flooding. Scrimgeour & Winterbourn (1989) found floods in the Ashley River disturbed stone surface organic layers and consequently affected primary production, community respiration and net community production of the epilithon. Nevertheless, they found that despite the unstable nature of the Ashley River, stone surface organic layers were present throughout the year. In the larger Rakaia River, epilithic algae were apparent during brief periods of stable flow, but stone surface organic layers were not visibly detectable in braids for extended periods. It seems likely that sparsely distributed particulate organic matter provided a important food for invertebrates during such times.

Patchy disturbance in braided rivers may further structure food quantity and quality by providing habitats varying in their quantities and proportions of terrestrial and instream energy inputs within the riverbed. In the Rakaia River, seepage streams tended to sustain higher algal abundances whereas braid substrates often showed no visible algal development. Particulate organic matter, therefore, may on average provide a greater proportion of food to invertebrates residing in the braids, while algae may become an increasingly important source to invertebrates living in seepage streams.

Following scour, recovering algae may be of higher quality in seepage streams as opposed to braids because of differences in the silt

content of developing algae in the pristine water of the spring and seepage streams compared to that in the typically discoloured braids. Graham (1988) studied the epilithic periphyton and possible interactions between periphyton and invertebrate consumers in the Waitaki River, which has a large alpine catchment and has water that is low in nutrients and is frequently clouded by fine inorganic silt. Graham (1988) found that periphyton on cobble substrates of the more stable side braids of the river accounted for most of the autotrophic production. He found no differences in photosynthetic rates between a stable discharge clear water tributary and the side braids, and attributed the often larger standing crop of periphyton in the mainstem to reduced macroinvertebrate grazing as a result of disturbance. However, he also observed that large amounts of fine inorganic silt particles were trapped within the periphyton of the main stem, whereas virtually no silt was present in periphyton in the stable discharge, clear water, tributary. The proportion of organic matter in periphyton is one measure of its food quality (Sloane - Richey *et al.*, 1981), and a high silt load reduces that proportion. Food quality can affect the growth rate, fecundity, size at pupation or emergence and number of emerging, aquatic invertebrates (Davies-Colley *et al.*, 1992). Thus Ryder (1989) cited in Quinn *et al.* (1992) found that growth of *Pycnocentroides* larvae (Trichoptera) confined to substrata with silted epilithon was 5.6 fold lower than growth of larvae on unsilted epilithon. Following flooding, recovery of periphyton in the clear waters of spring and seepage streams of the Rakaia may result in the occurrence of a higher quality food source than in the neighbouring braids. In contrast, perennial seepage streams

may retain unscoured but silted organic layers, and as a consequence may suffer reduced food quality.

Distribution of invertebrates sometimes closely reflects the distribution of their food source. For example Egglshaw (1964) demonstrated a close relationship between many benthic invertebrates and the distribution of detritus in two streams in the Scottish highlands. Rabeni & Minshall (1977) also demonstrated experimentally that some stream insects colonised small (1 - 3.5 cm) substrata primarily because they were most efficient at collecting the fine detritus that represented the insects' main food. In the Rakaia, density of Chironomidae was strongly correlated with algal abundance ( $r_s=0.70$ ,  $p<0.001$ ) followed closely by FPOM ( $r_s=0.66$ ,  $p<0.001$ ), both of which were more common in seepage streams, however Deleatidium larval density appeared only weakly associated with FPOM ( $r_p=0.30$ ,  $P<0.001$ ), and algal abundance ( $r_s=0.27$ ,  $P<0.01$ ), and cobbles ( $r_p=0.28$ ,  $P<0.01$ ). The single greatest proportion of Deleatidium densities was in fact best explained by vertical hydraulic gradient (table 10). This might have been partly because their densities reflected ovipositional preferences that coincided with upwelling, slower flowing sites, where FPOM had accumulated.

McLean (1967) recorded that female imagos of some species of Ephemeroptera in a North Island stream appeared to select oviposition sites which could influence the subsequent distribution of larvae. For example, imagos of the mayfly Zephlebia cruentata (= Acanthophlebia

*cruentata*) oviposited along the margins of quiet pools, whereas *Coloburiscus humeralis* males were observed to swarm over riffles, and females to oviposit within them. Likewise, Collier (1994) considered that settling and subsequent hatching of eggs in slow flowing areas may be a factor influencing the distribution of *Deleatidium* mayfly nymphs in rivers. Positive values for vertical hydraulic gradient were synonymous with smooth surface flows and indicated areas often ideal for settling and hatching of eggs in the shallow parts of seepage streams.

### **Habitat complexity as a result of disturbance**

Frequent and unpredictable flooding has a direct role in determining habitat complexity in a braided river, as the formation of seepage and spring streams is dependent on flooding (Rundle, 1985). However frequent and unpredictable, flooding may also have an indirect role in determining levels of invertebrate production by sporadically changing various aspects of habitat complexity in the braids and seepage streams. For example, some chironomids burrow into algal mats or live among filamentous algae in these channels, so the loss of algae through scouring will reduce habitat available to chironomids and hence lower chironomid production in such areas. A further example is that subsurface interstices which can be important habitats for invertebrates (e.g. Huryn, 1996b; Adkins, 1997), and a source of recolonists following disturbance (Brunke & Gonser, 1997), may change dramatically in structure and extent within a single flood event.

The continually reworked bars in the central riverbed where the spring fed streams occur, may provide a locally extensive, interstitial habitat (e.g. Figure 6 b), but in the absence of bed disturbance, this habitat may become progressively unavailable as silt and fine sand is deposited. Silt can reduce the quantity and degrade the quality of the interstitial habitat by infilling interstitial volume, and restricting water flow within the interstices (Davies-Colley *et al.*, 1992). Nevertheless, I occasionally found benthic macroinvertebrates including early instar Deleatidium spp., and hypogean species such as Phreatogammarus fragilis present at a depth of up to 400 mm at some silted sites. I also found clean pea gravel deposits at sites such as recently reworked or scoured bars particularly in association with subsurface water erosion (e.g. springs and seepages) and at times they contained high densities of early instar Deleatidium.

In conclusion, it seems likely that the conditions associated with seepage streams are most conducive to rapid accumulation of juvenile Chironomidae and Deleatidium for a multiplicity of reasons. Organic material inputs and their quality may set the upper limit of secondary production under optimal conditions, however, production is normally regulated at some level below this limit by patchy flow - mediated disturbances, such that distributional patterns reflect survivorship of invertebrates, but more often, varying rates of recovery within the river bed.

## CHAPTER FIVE

### CONCLUSION

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Production varies substantially between the various habitats of a braided river, and is consistently highest in seepage stream microhabitats within "flood overflow" channels. Production values for Deleatidium in the seepage streams are among the highest for Deleatidium in the South Island. Research from this study and by Hughey et al (1989) indicates that production between  $2.6 - 7.7 \text{ g m}^{-2} \text{ yr}^{-1}$  may be expected for Deleatidium in the seepage streams of the various foothills and alpine catchment braided rivers in Canterbury. Although production of Deleatidium in the seepage streams of the Rakaia was at the lower end of the scale, production of Aoteapsyche and Chironomidae was relatively much higher than that calculated from data obtained by Hughey *et al.* (1989) in the Waimakariri or Ashley Rivers. Consequently, while species composition changed, total production in the seepage streams was similar in the three rivers ( $3.2 - 10.3$ ;  $8.3$ ;  $8.3$ ;  $\text{g m}^{-2} \text{ yr}^{-1}$ , respectively). In contrast to the seepage streams, total production in the braids was highest in the Ashley, intermediate in the Waimakariri, and extremely low in the Rakaia ( $5.3 - 4.4$ ;  $2.2 - 1.7$ ;  $0.6 - 0.5 \text{ g m}^{-2} \text{ yr}^{-1}$ , respectively). However, production particularly in the braids, is likely to vary greatly from year to year in each of the rivers because of variation in rainfall within their catchments.

Deleatidium production also varies seasonally (Winterbourn, 1973), both within and between the foothills and alpine catchment braided rivers

(Scrimgeour, 1987; Hughey, *et al.*, 1989). In the alpine fed rivers, 'winter cohort' production appears particularly important in the braids, and the seasonal accrual of invertebrates appears to culminate at the onset of the wrybill breeding season. However, flood limited 'summer cohorts' in the braids may be greatly exceeded in seepage streams protected from the smaller of the spring - summer spates (e.g. Waimakariri River: Hughey *et al.*, 1989). At the onset of spring to summer floods, these seepage streams would likely provide the most important foraging areas for wading birds such as the wrybill.

It seems likely that the conditions associated with seepage streams are most conducive to especially rapid accumulation of juvenile Chironomidae and *Deleatidium* for a multiplicity of reasons. Seepage streams are shallow, and usually have beds dominated by gravels and cobbles, packed with coarse to fine sands near to, if not flush with the surface, nevertheless, where sand has been flushed from the substrate, bed material can be very porous. These streams tend to retain flood debris and may provide shelter for periphytic communities and invertebrates from relatively small scale scouring flows. Data from the Waimakariri, Ashley, and Rakaia Rivers, suggest that differences in densities of insects between seepage streams and braids may largely reflect varying rates of success of larvae recruited via oviposition and egg hatching rather than drift, which has been shown to be an important recolonisation mechanism in the braids (Sagar, 1983a). This appears to support the suggestion by Scrimgeour, Davidson, & Davison (1988), that

minor braids, but also seepage streams, provide a colonisation epicentre to the larger riverbed after severe bouts of flooding. Catastrophic drift of similar aged cohorts of insects in the braids means that those surviving in the seepage streams are likely to contribute strongly to the overall secondary production of the river.

Ultimately, flooding and its geomorphological expression structures the various habitats and creates the seepage and spring streams. Rundle (1985) indicated that the maintenance of seepage streams in the Rakaia River is also dependent particularly on large floods that can induce dramatic changes in the pattern of braiding. Similarly, Glova & Duncan, (1985) indicated that these types of channels can be vulnerable to dewatering. My data further suggests that the 'best quality' seepage and spring stream habitats have to be scoured frequently to remove silted epilithon, accumulating silt, and sand, and that large scale cut and fill events are important in maintaining pore spaces, which provide additional habitats for the epigeal fauna. Therefore, management that alters a braided rivers discharge regime will likely affect the frequency, distribution, and quality of seepage and spring stream microhabitats, which have an important role in braided river ecology.



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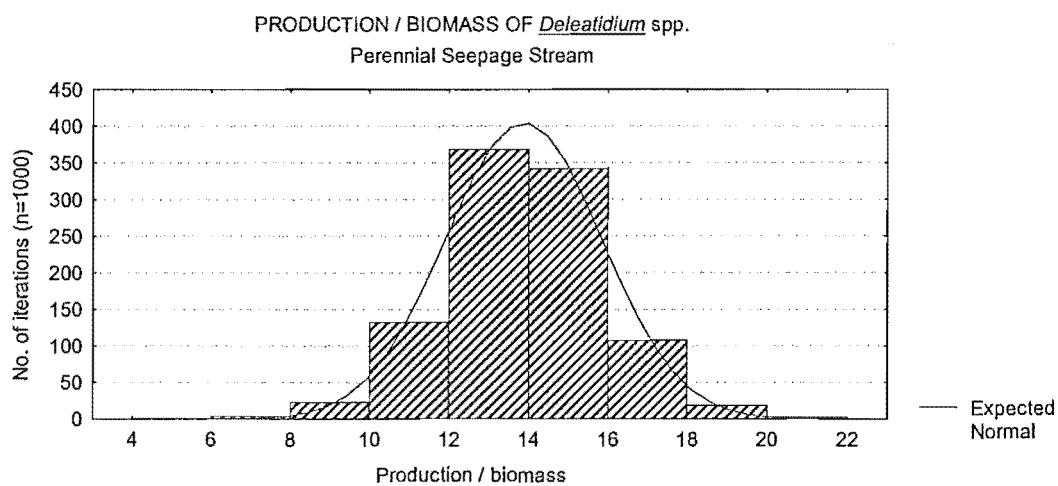
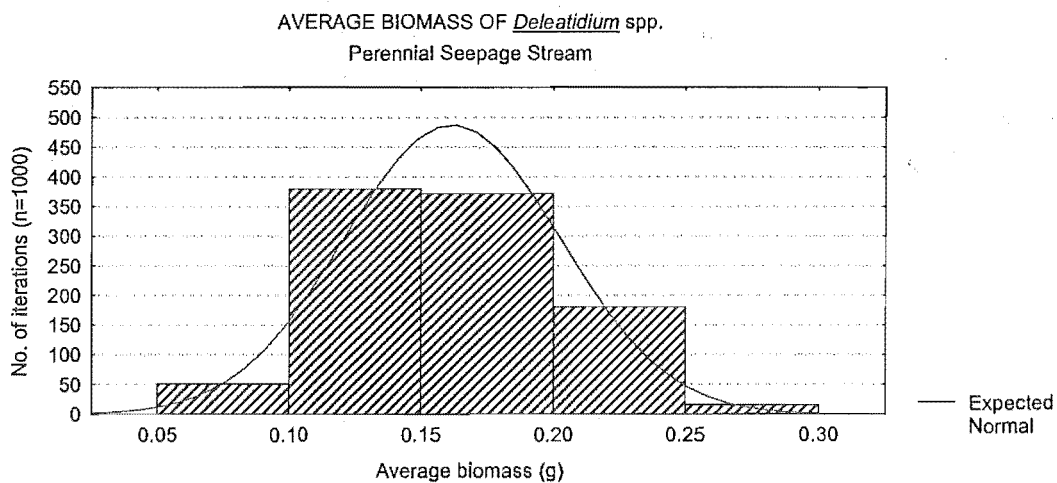
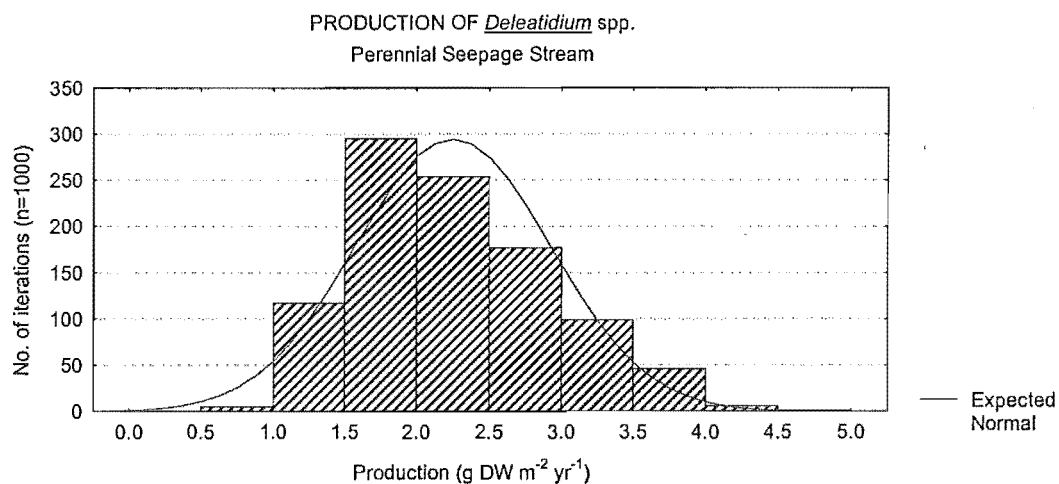
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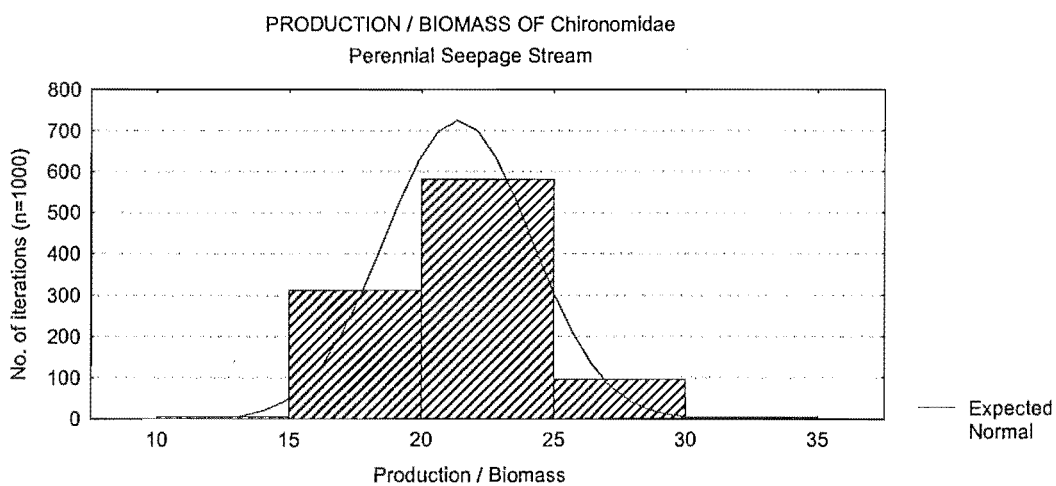
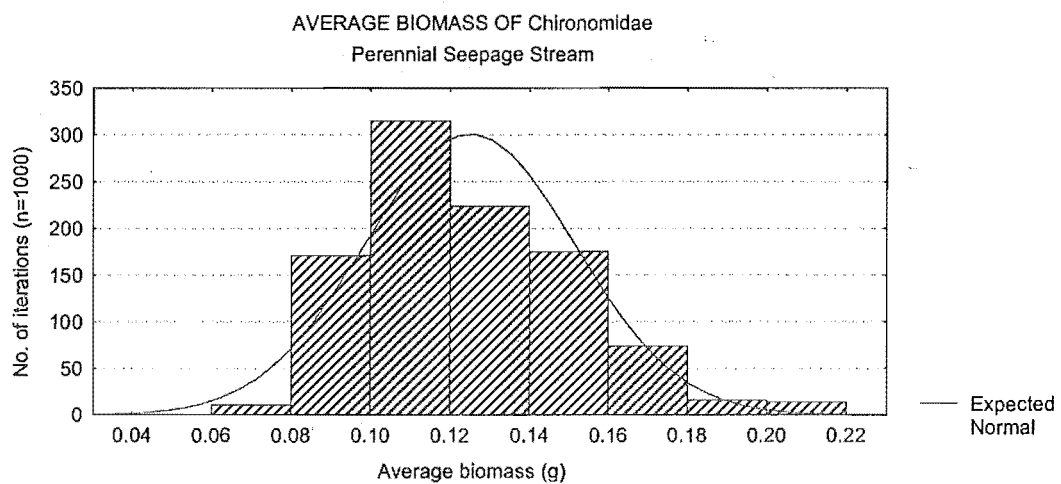
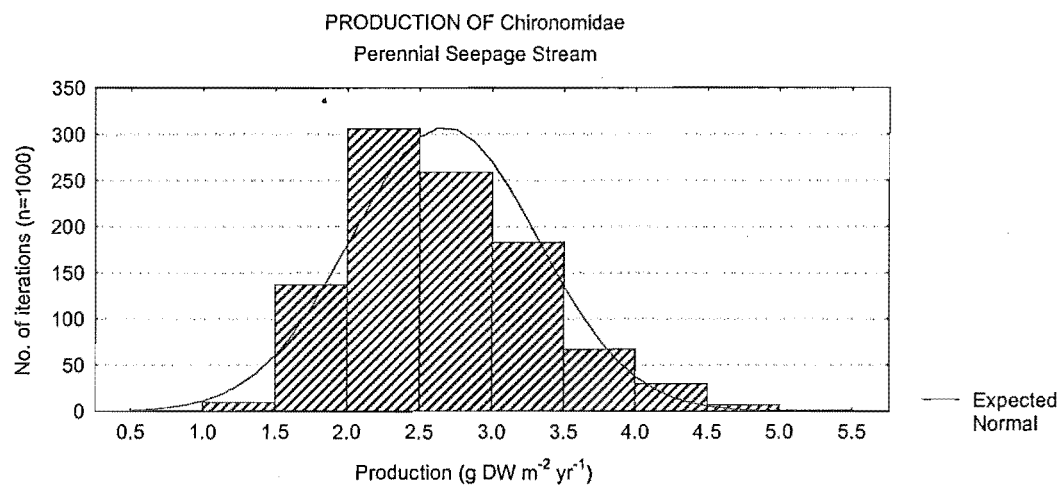
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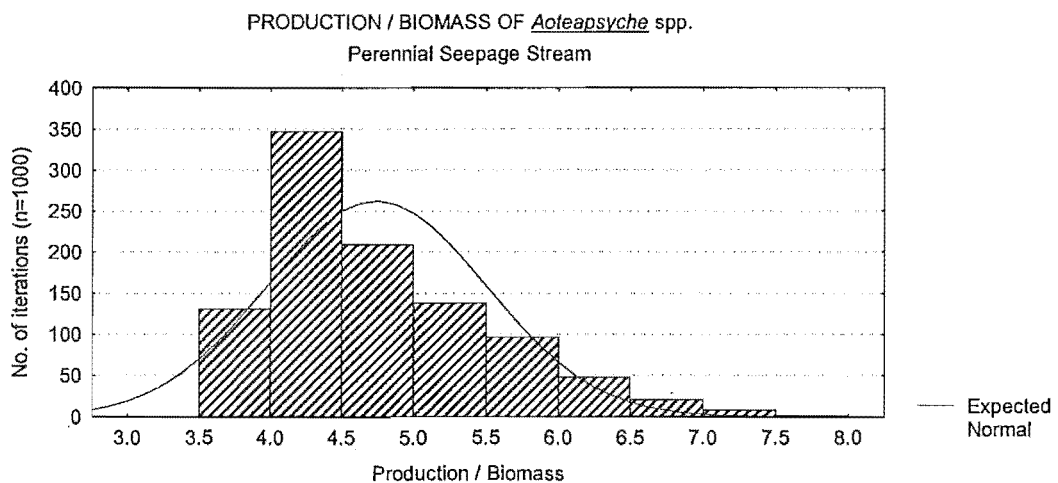
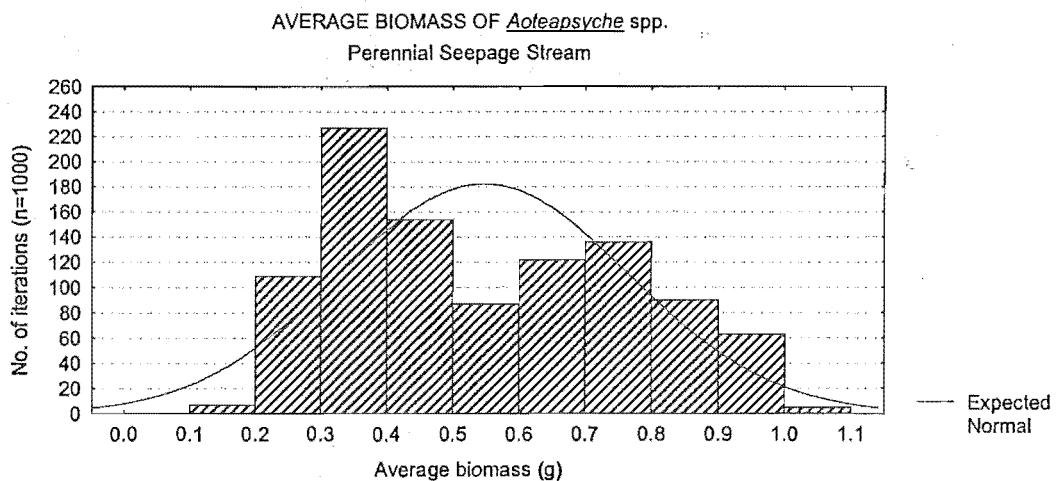
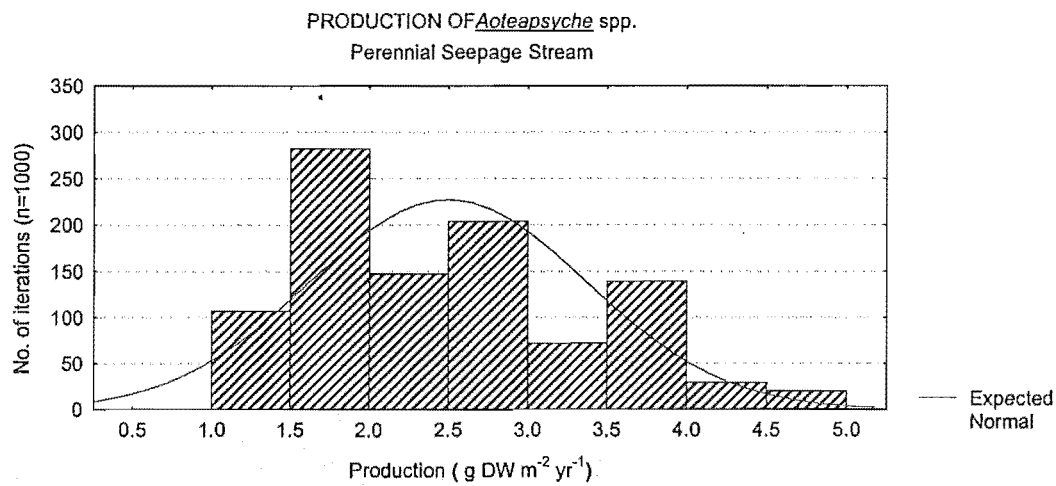
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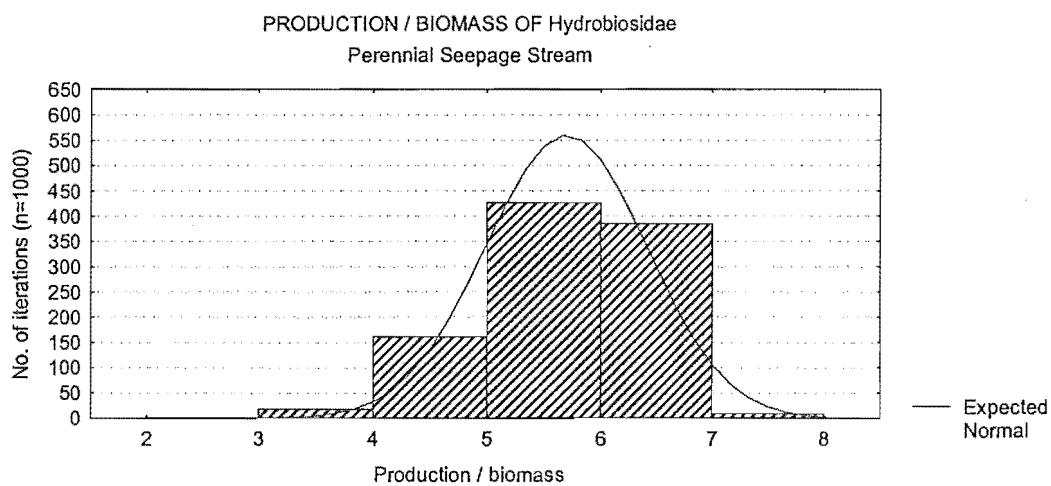
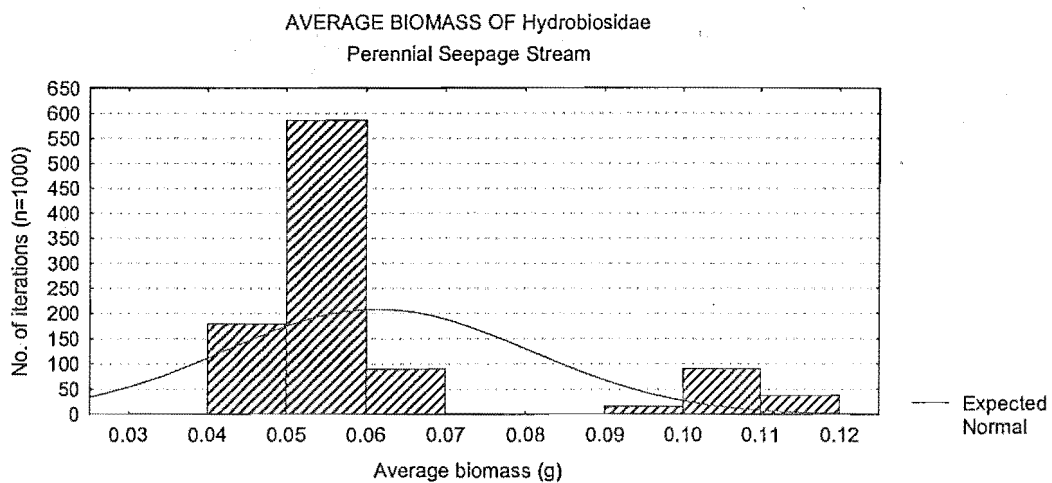
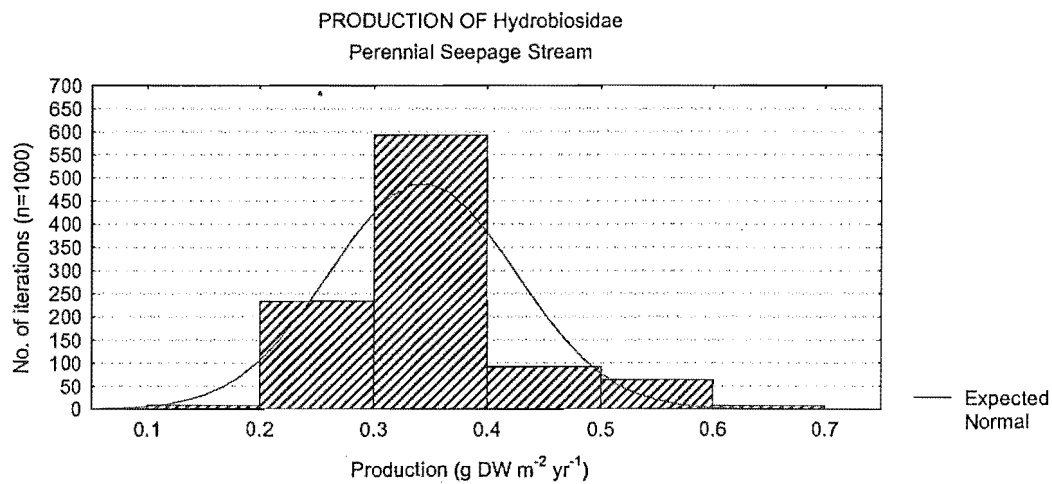


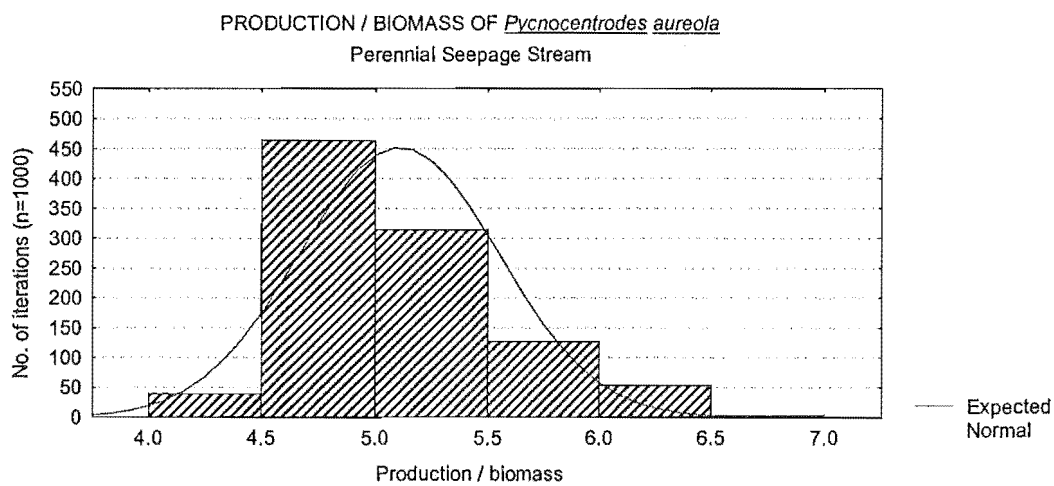
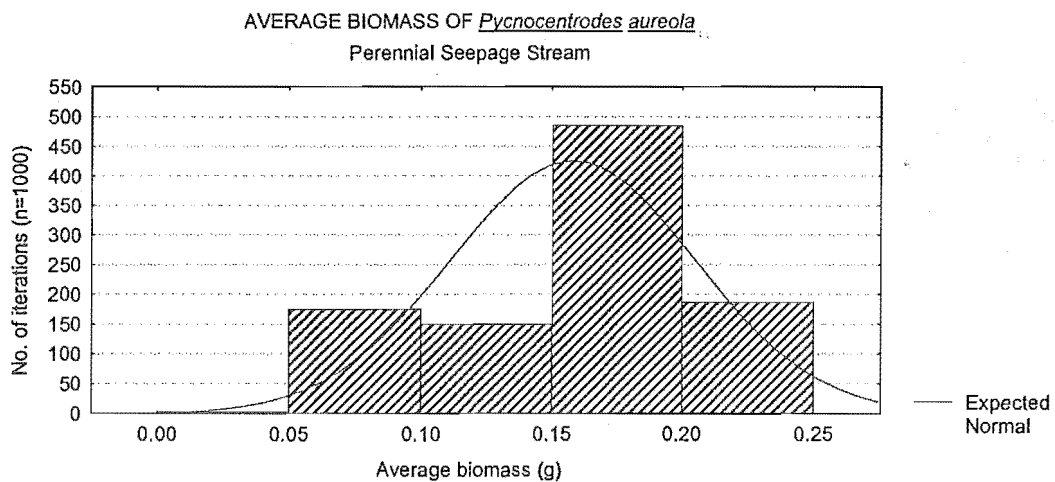
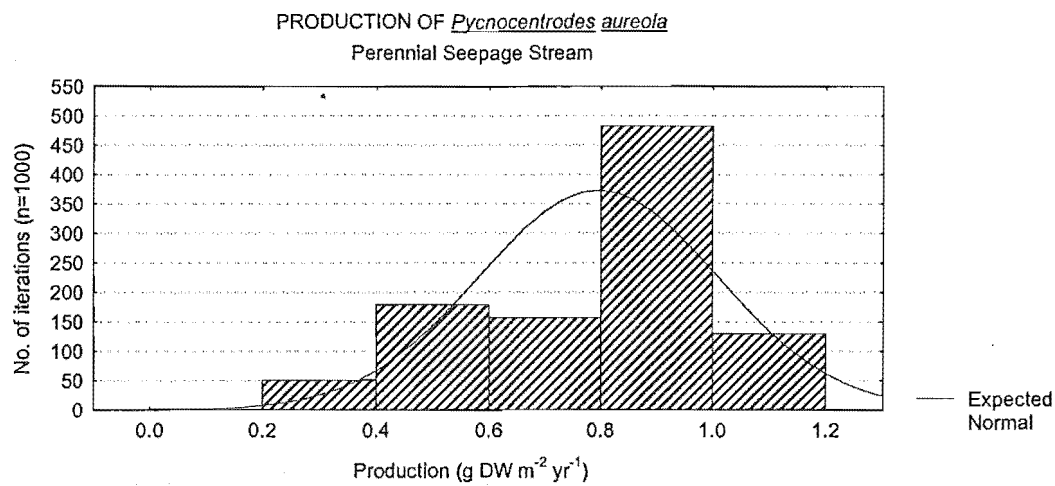


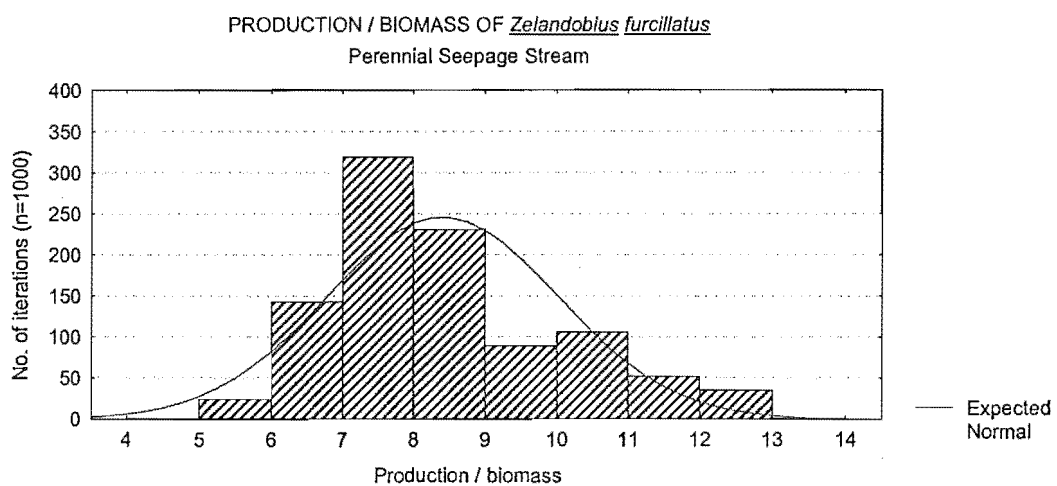
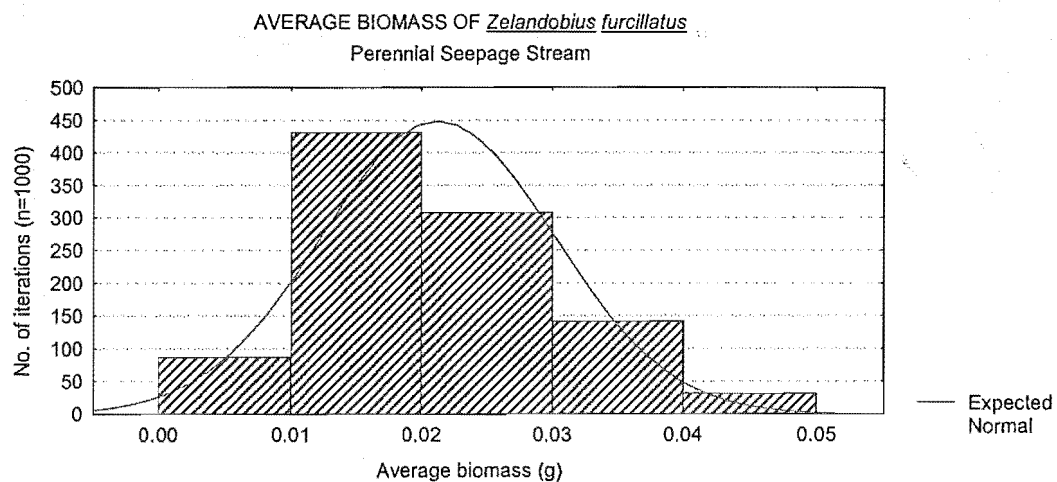
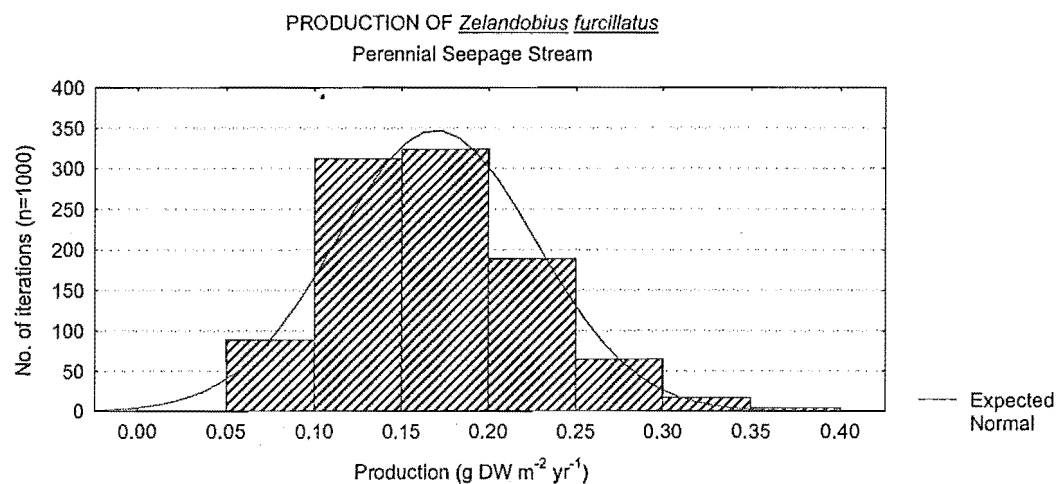


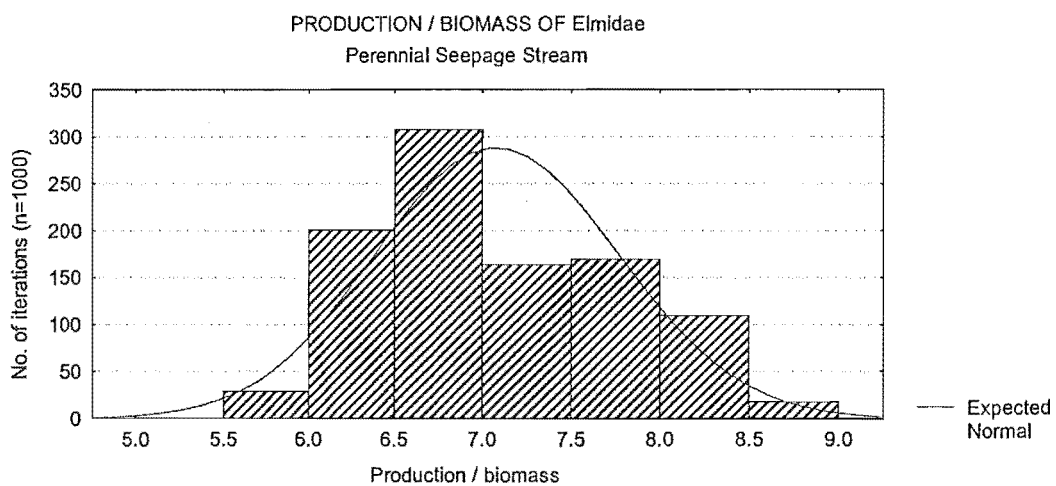
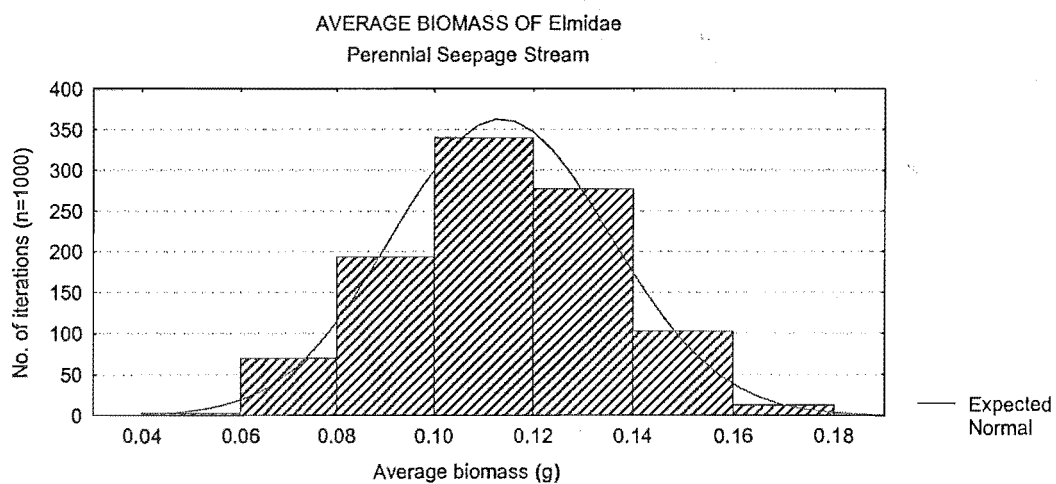
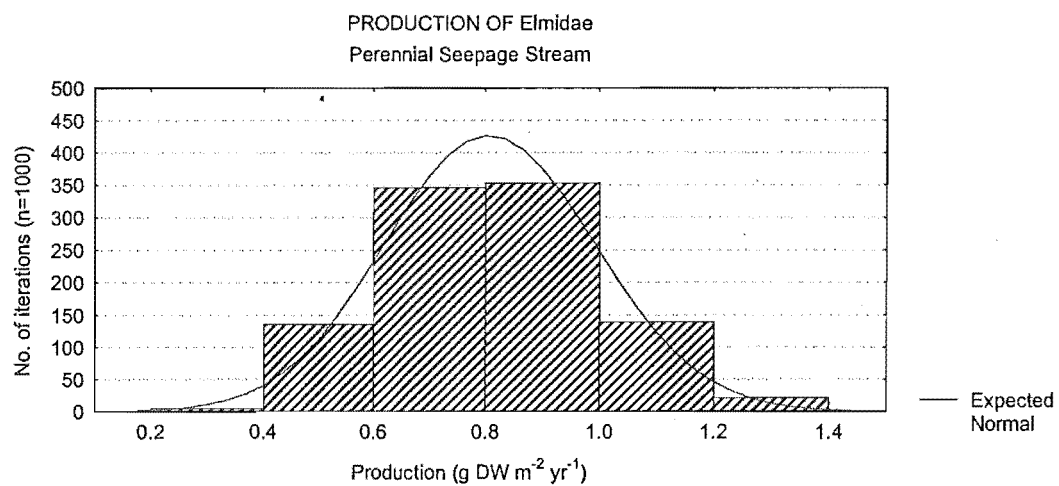


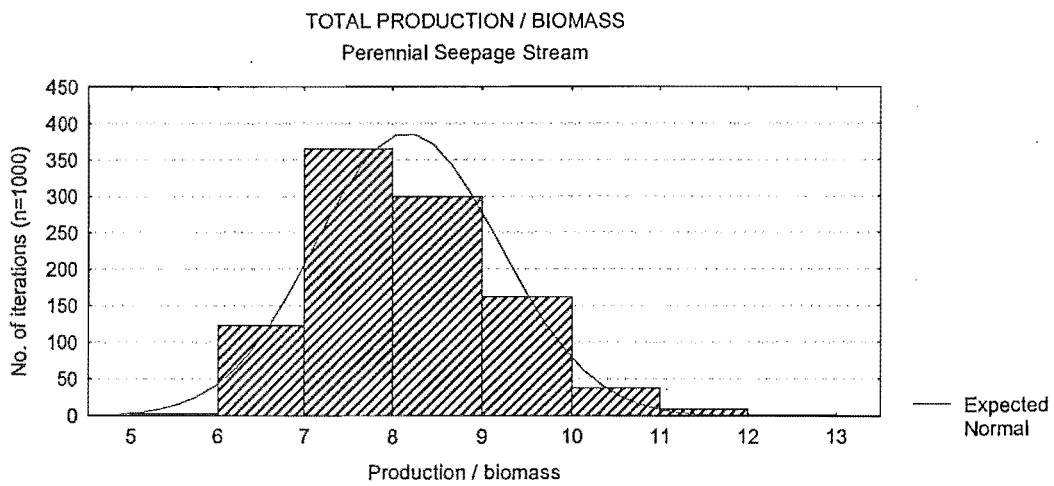
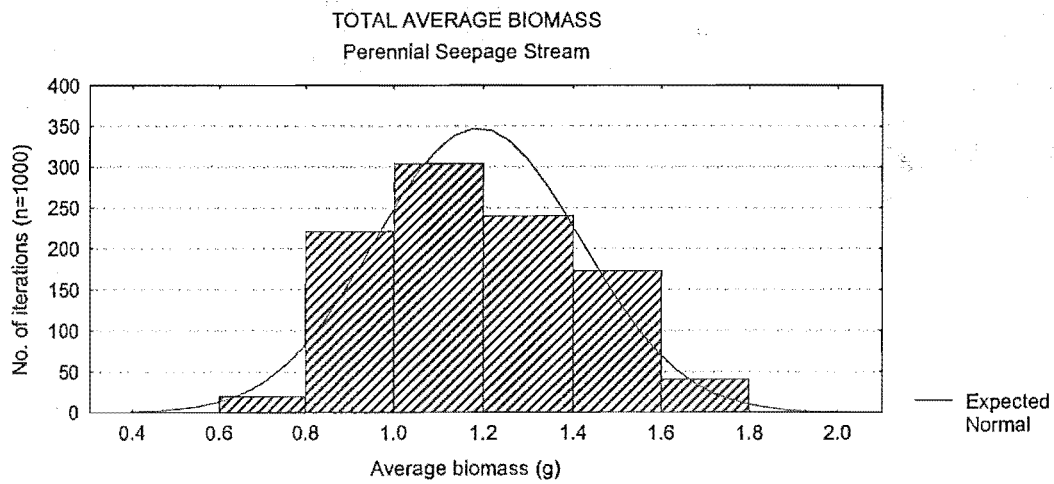
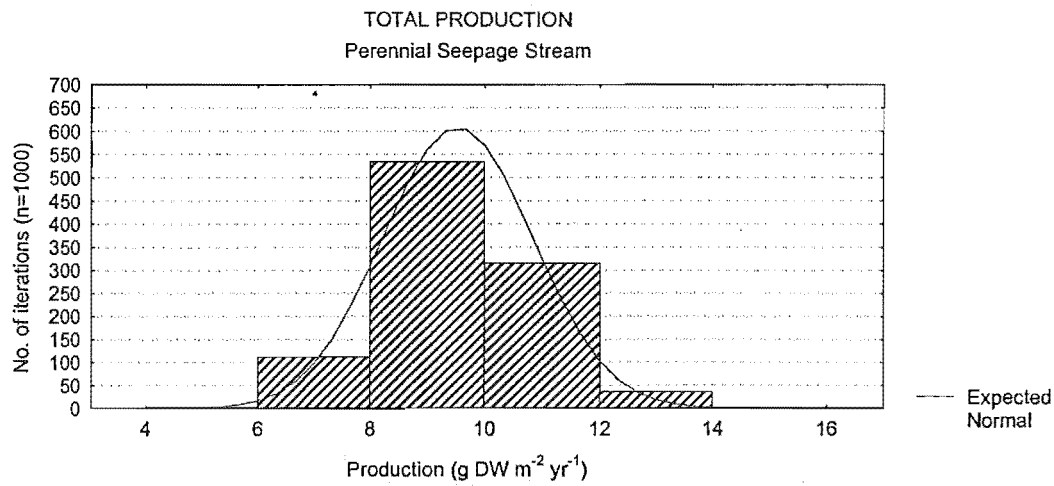




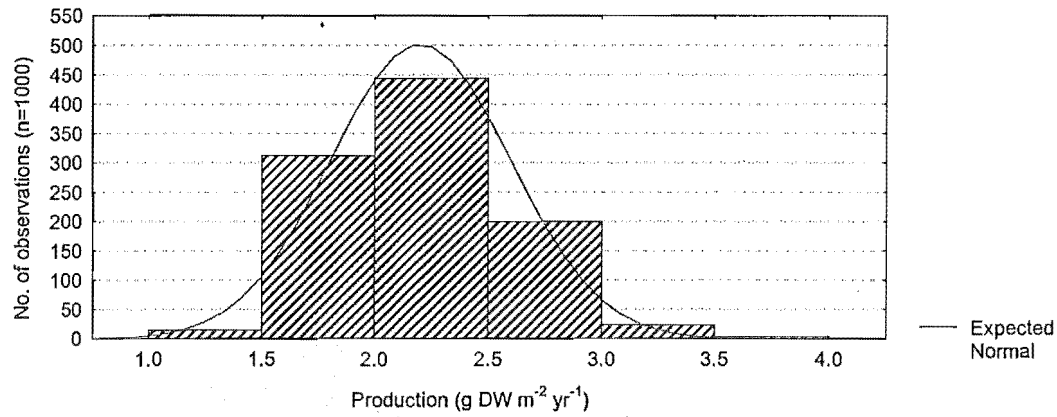




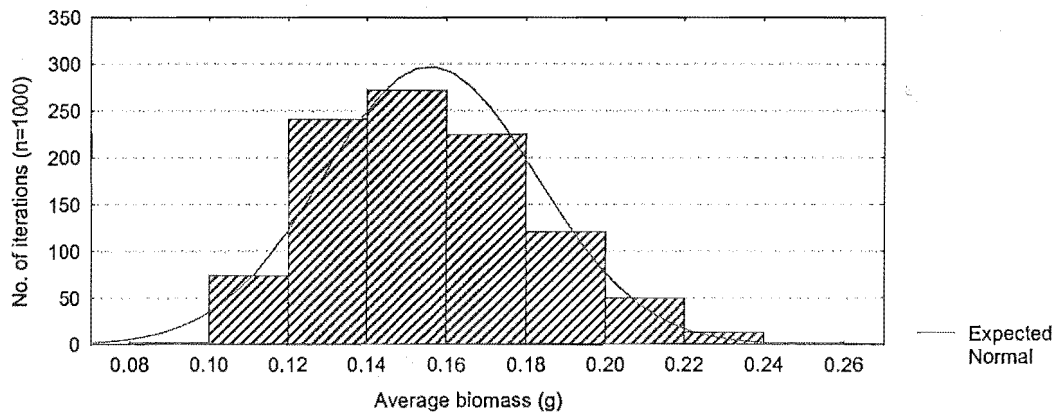




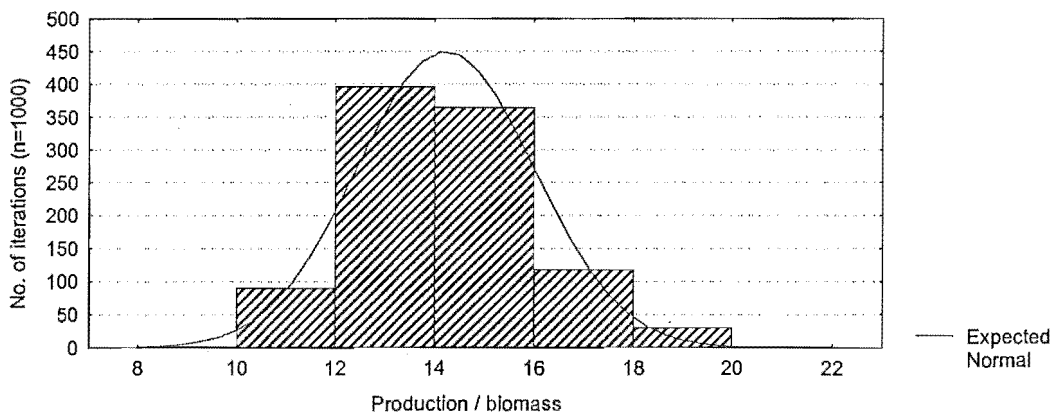
PRODUCTION OF *Deleatidium* spp.  
Baseflow Seepage Stream

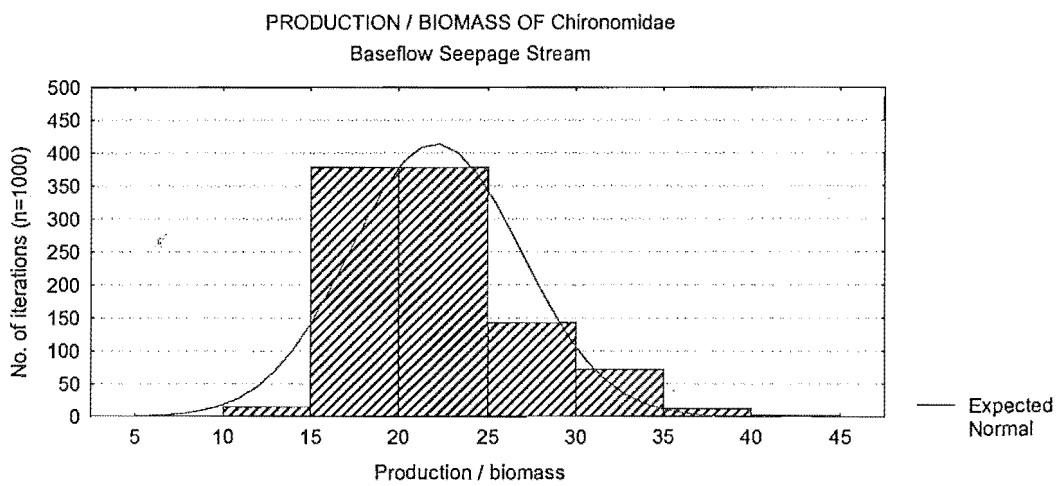
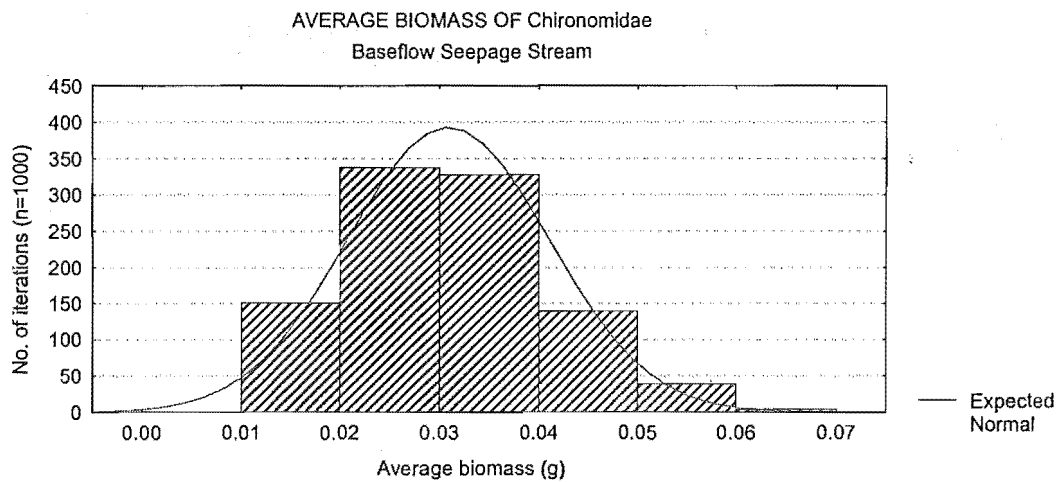
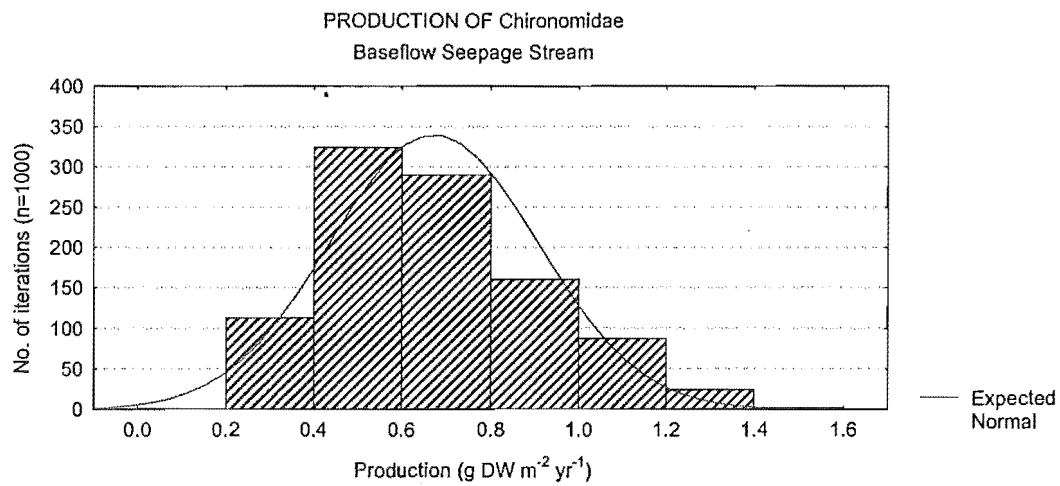


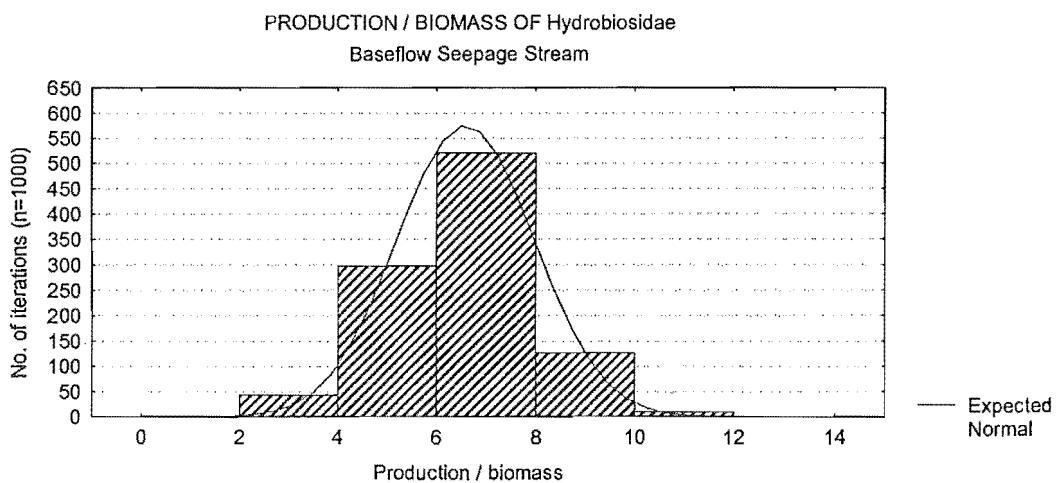
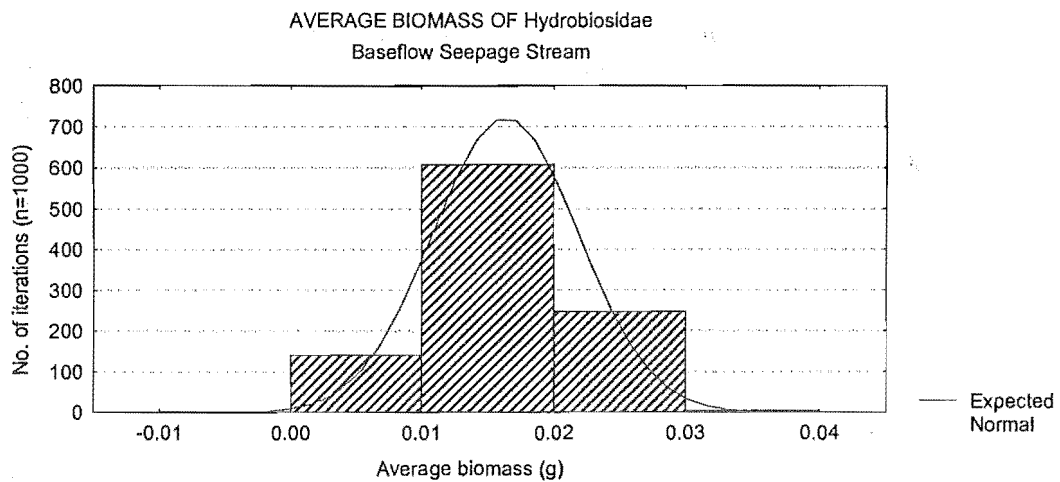
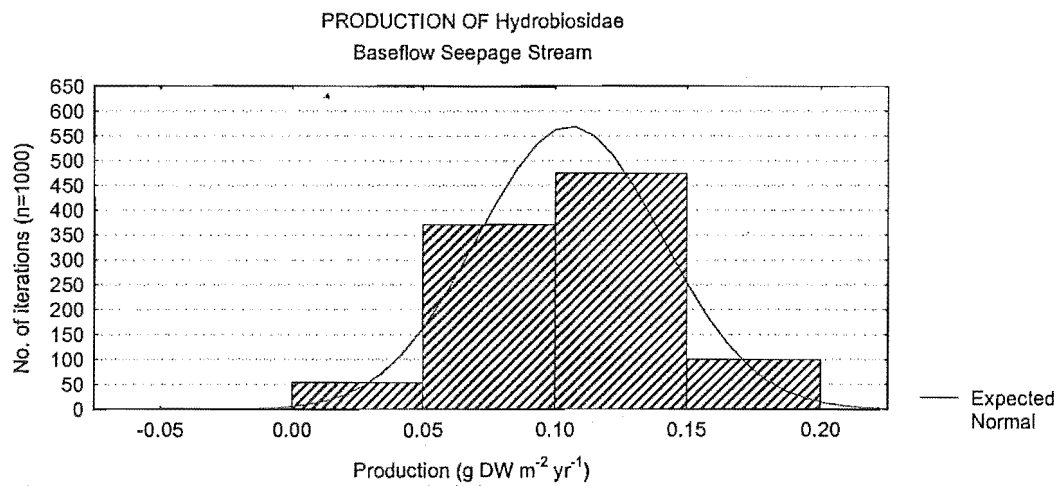
AVERAGE BIOMASS OF *Deleatidium* spp.  
Baseflow Seepage Stream



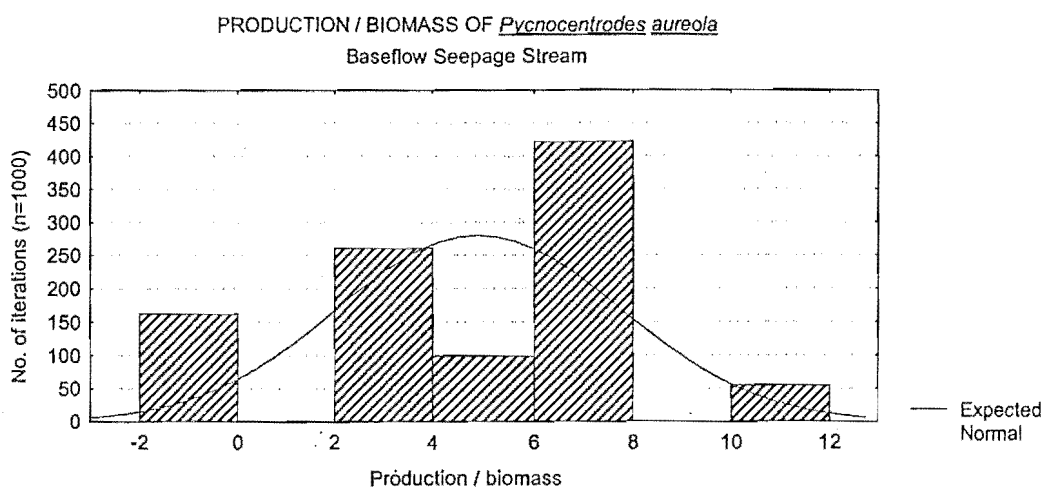
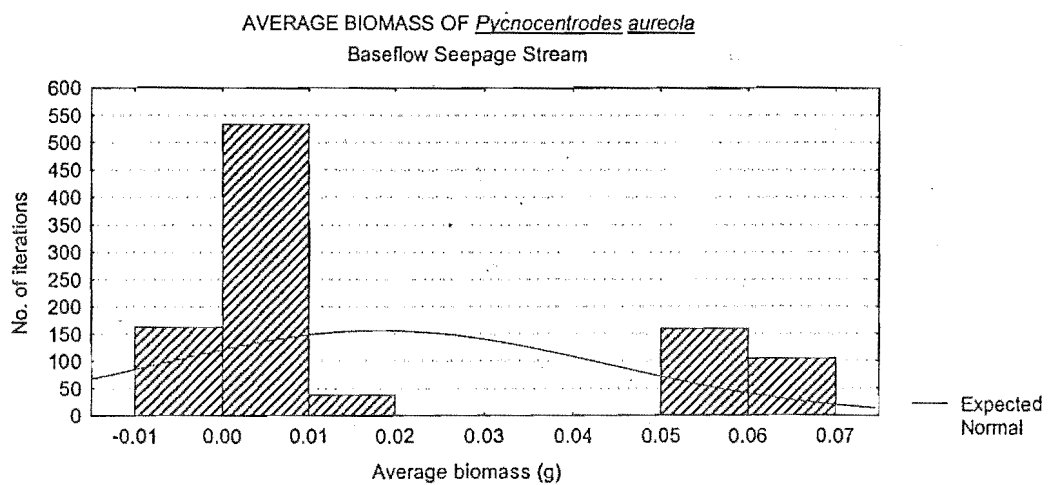
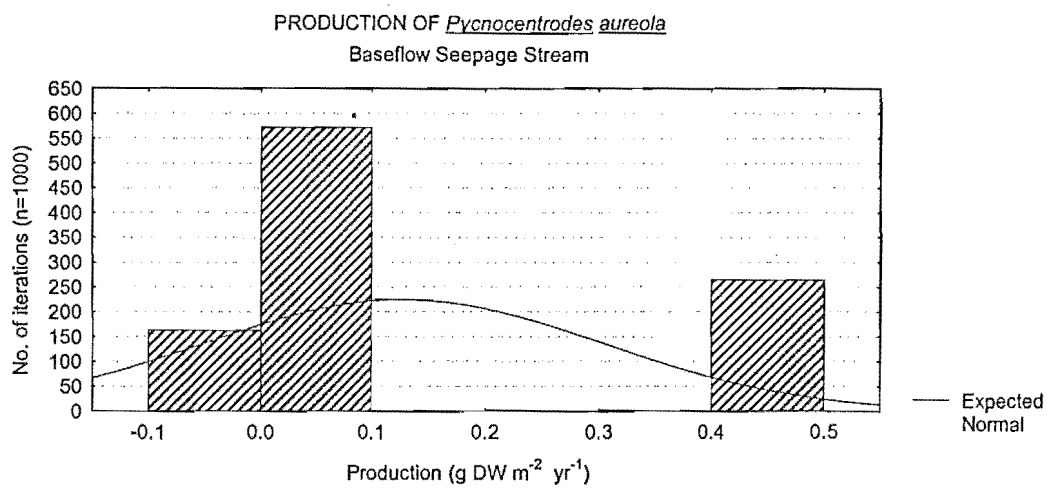
PRODUCTION / BIOMASS OF *Deleatidium* spp.  
Baseflow Seepage Stream

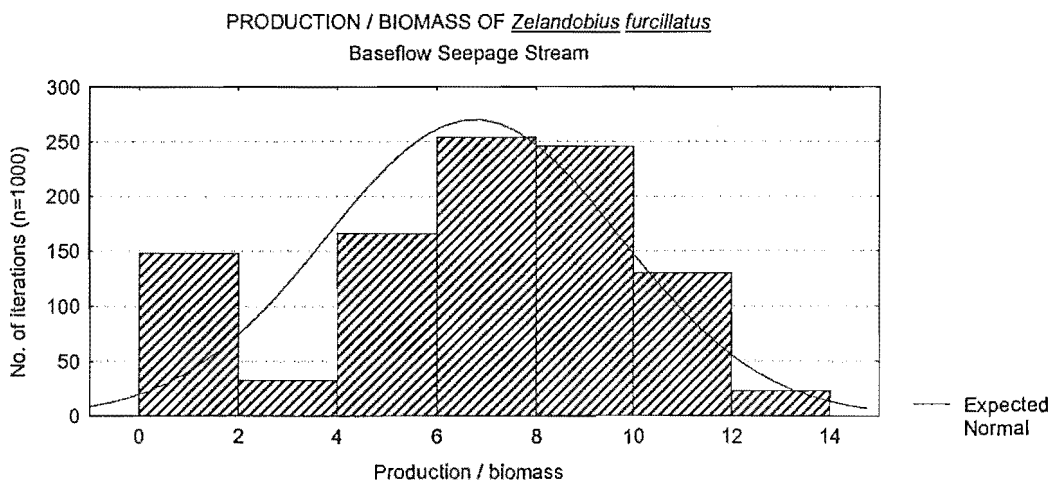
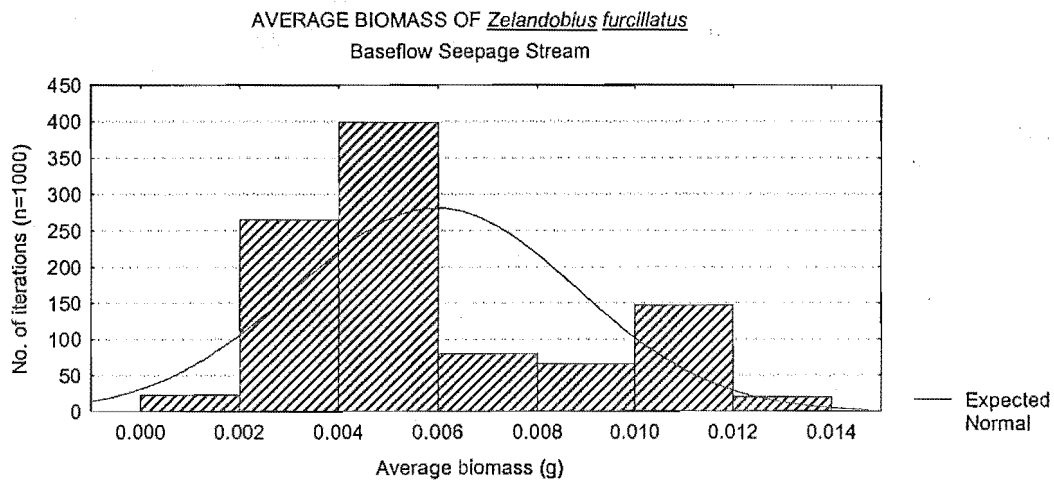
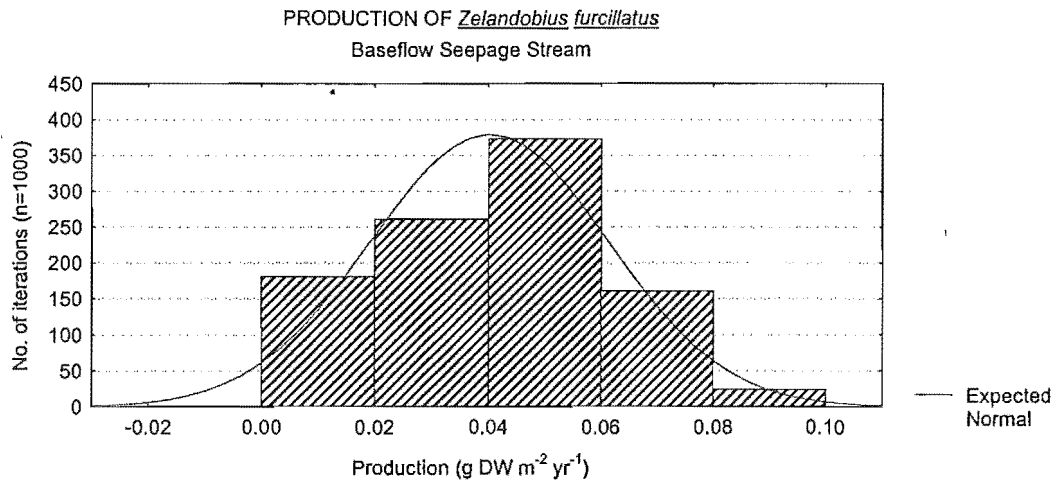


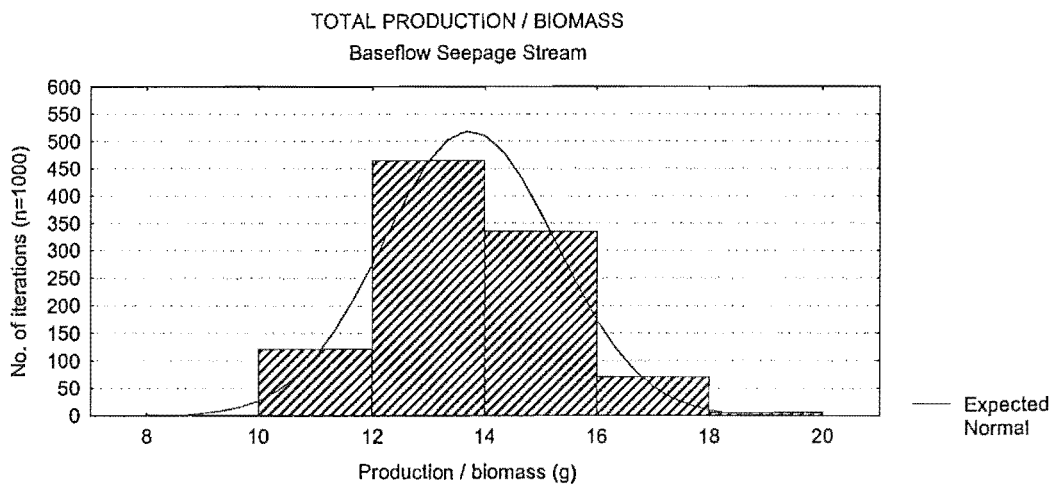
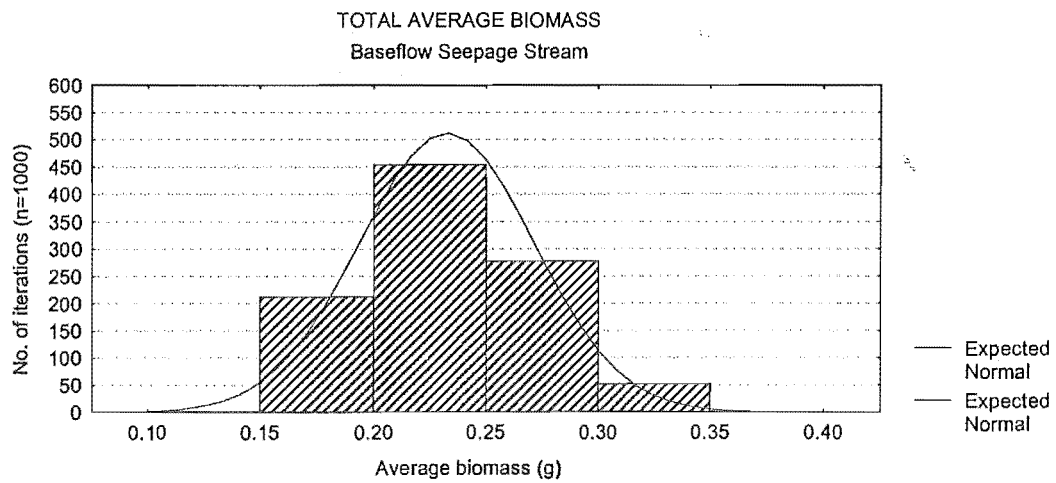
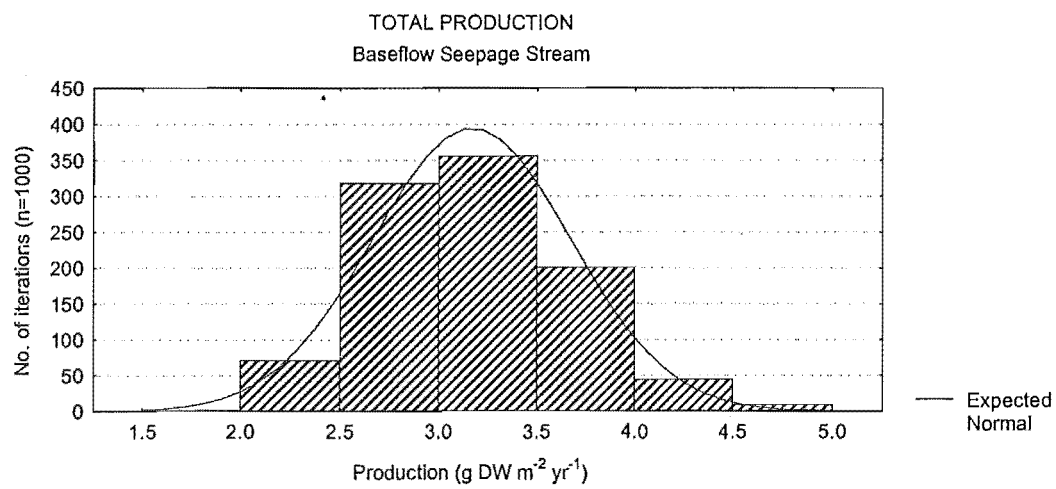


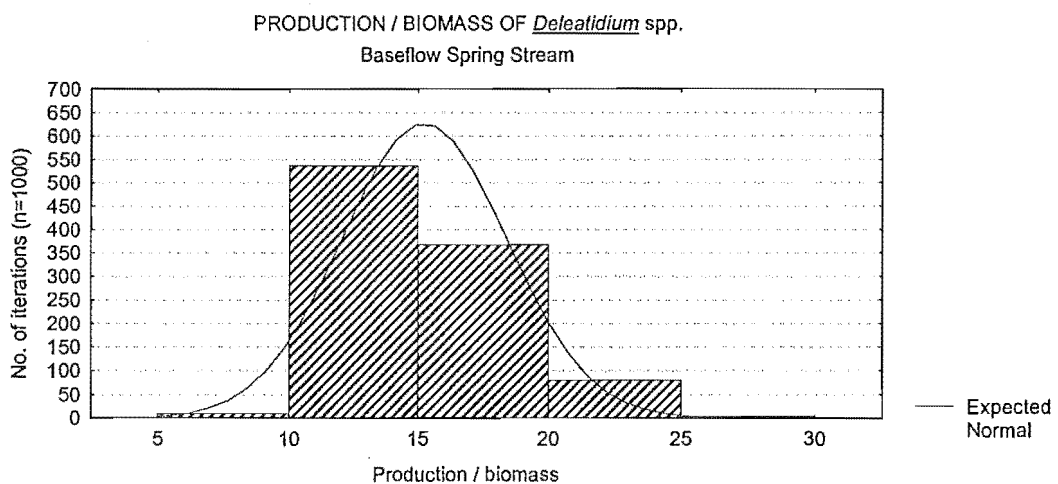
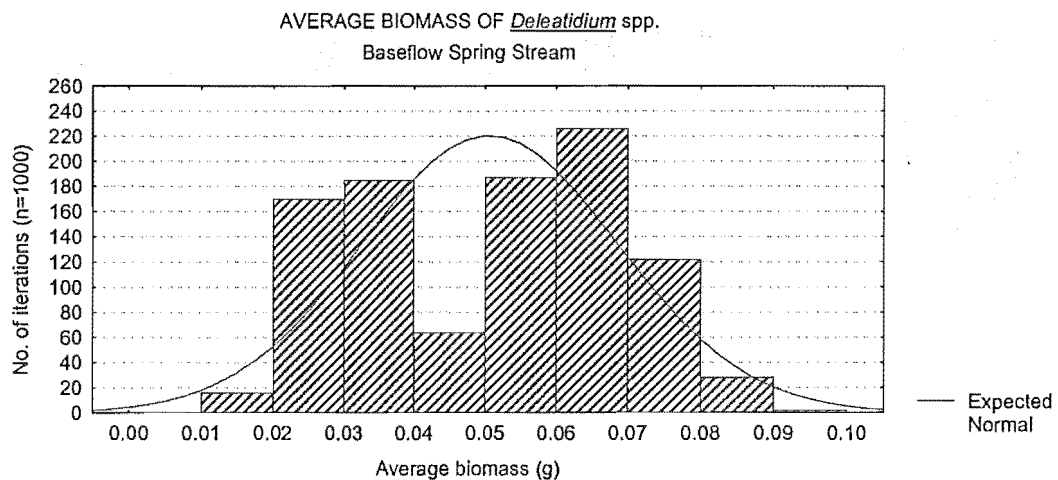
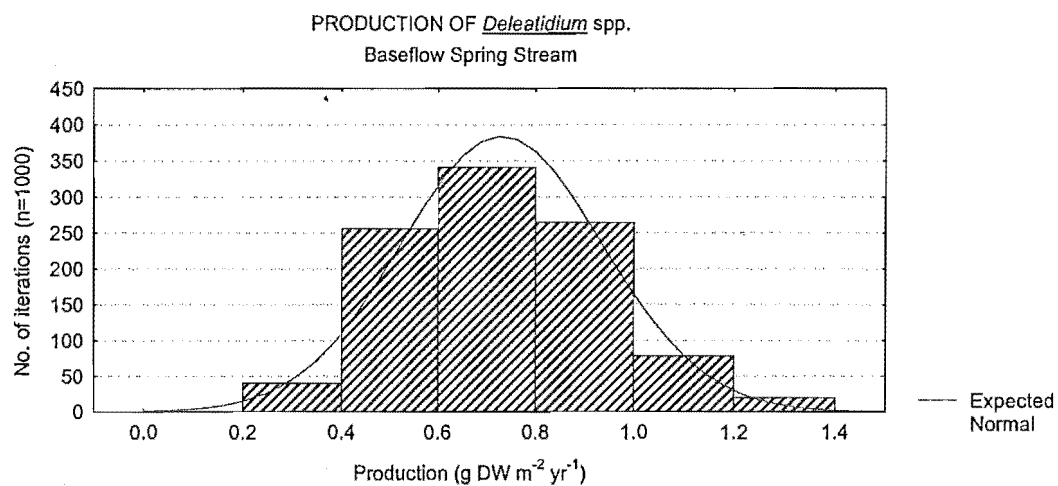


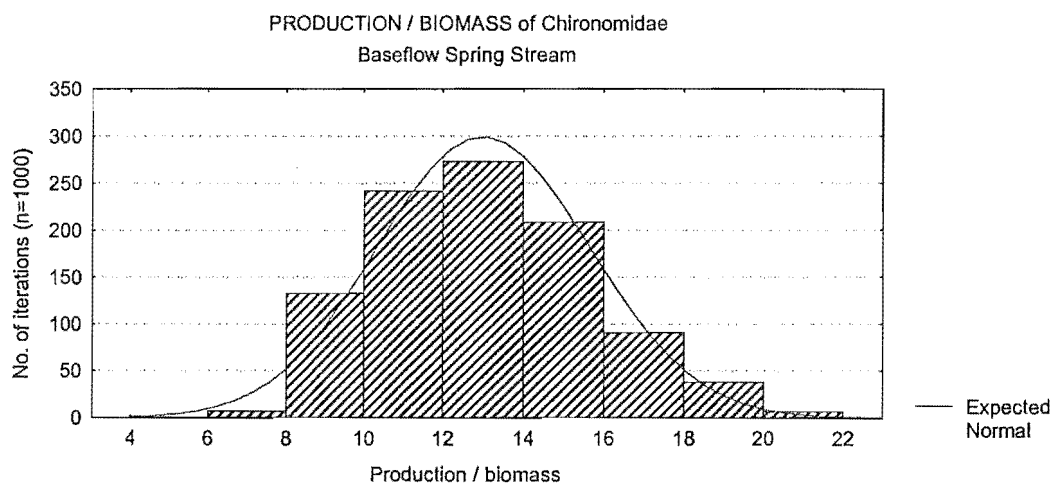
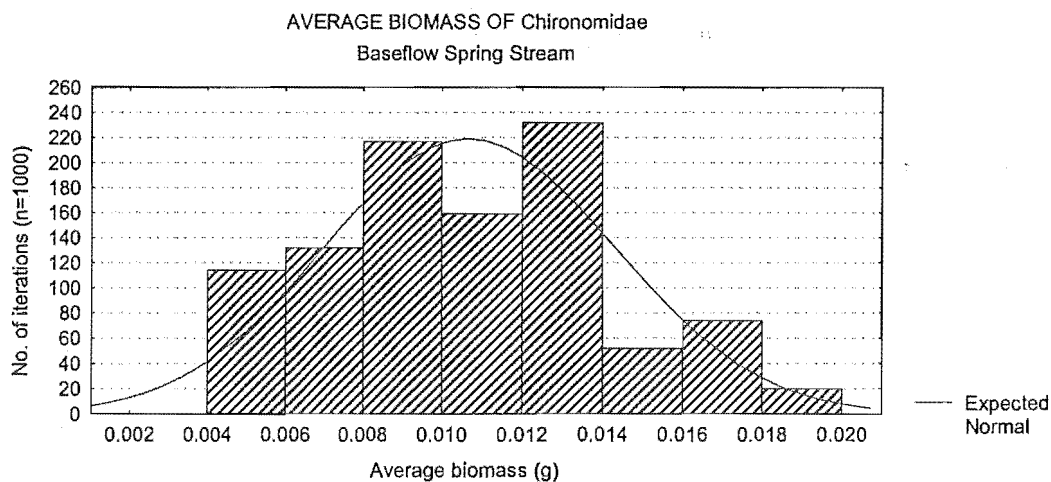
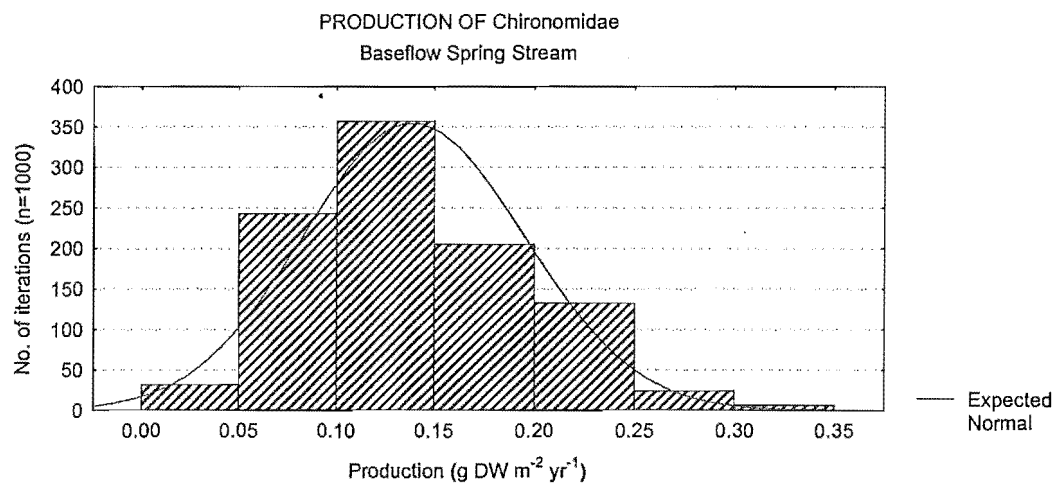


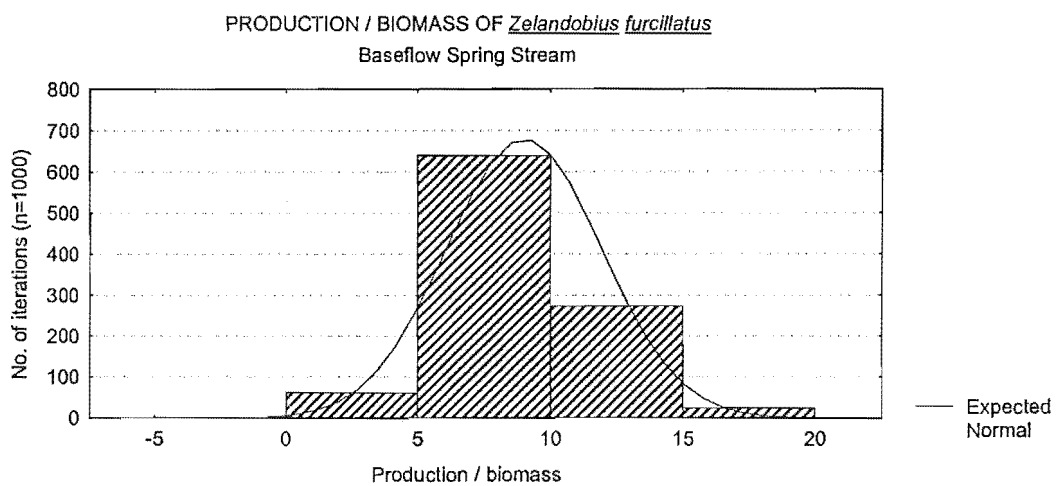
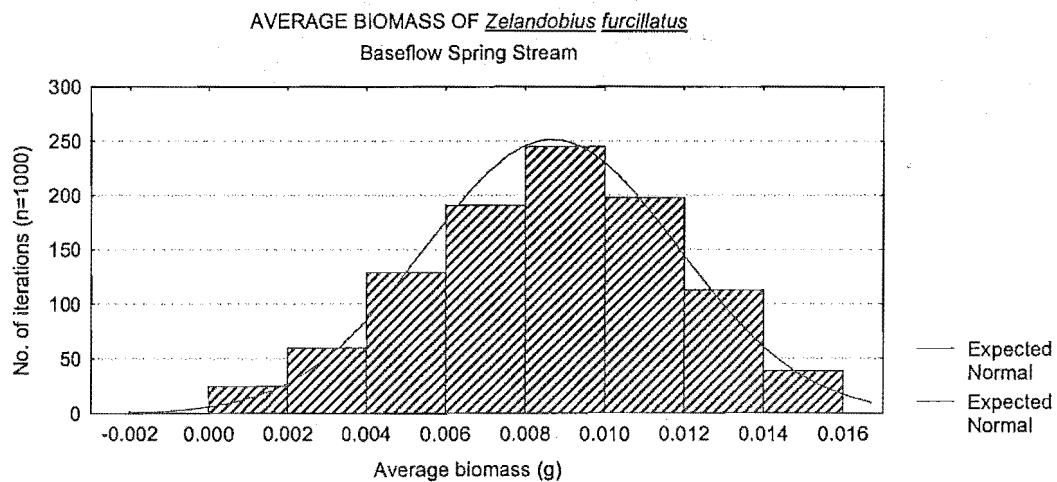
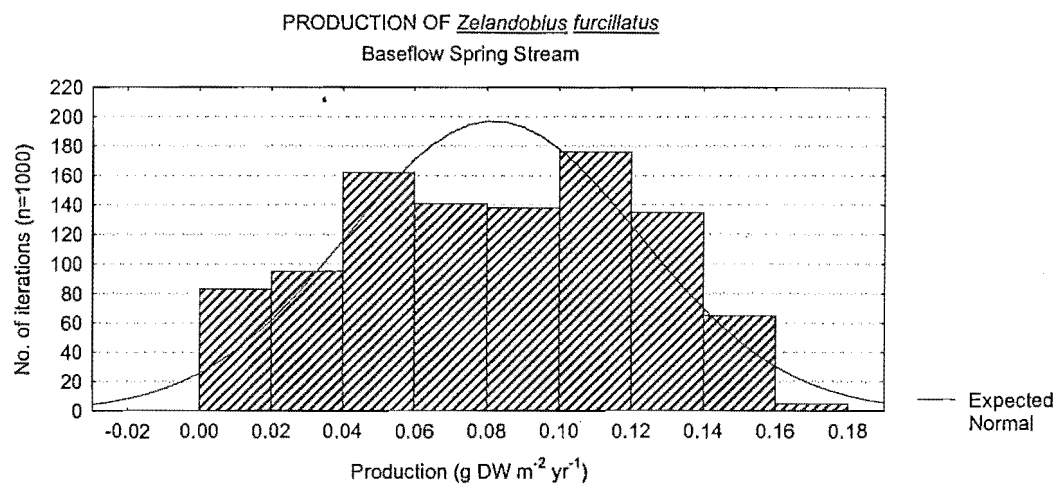


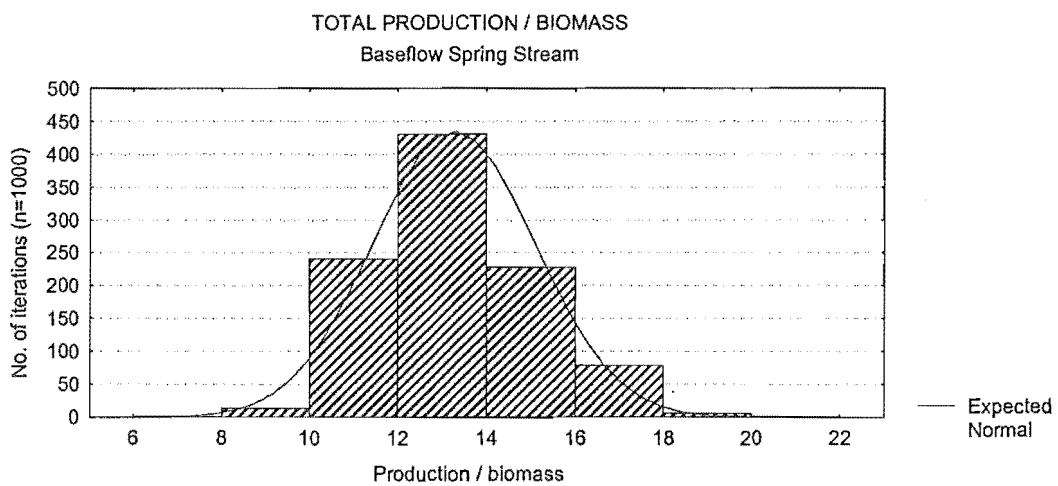
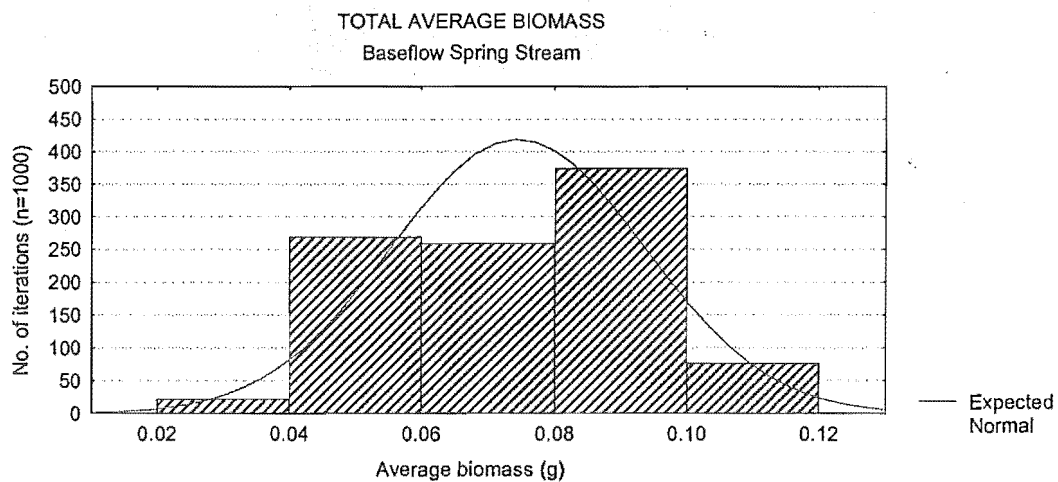
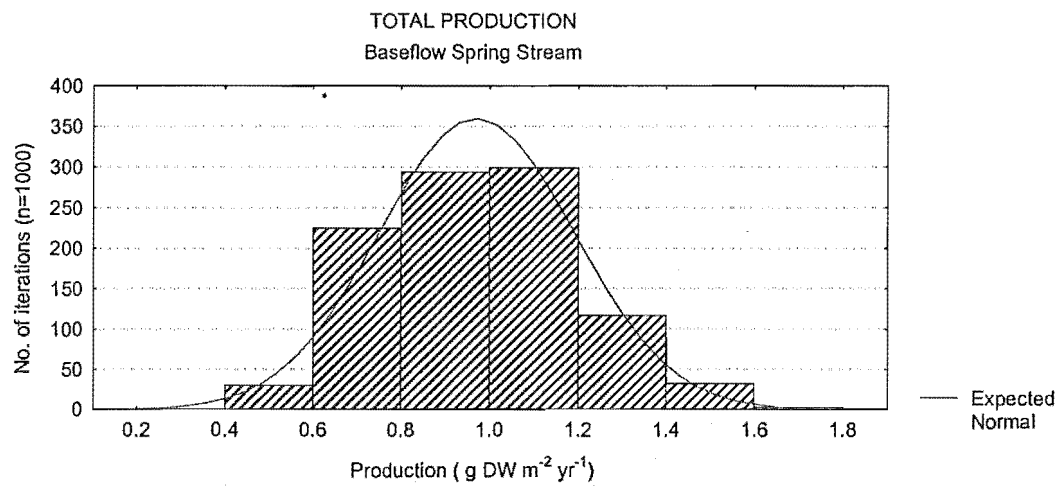


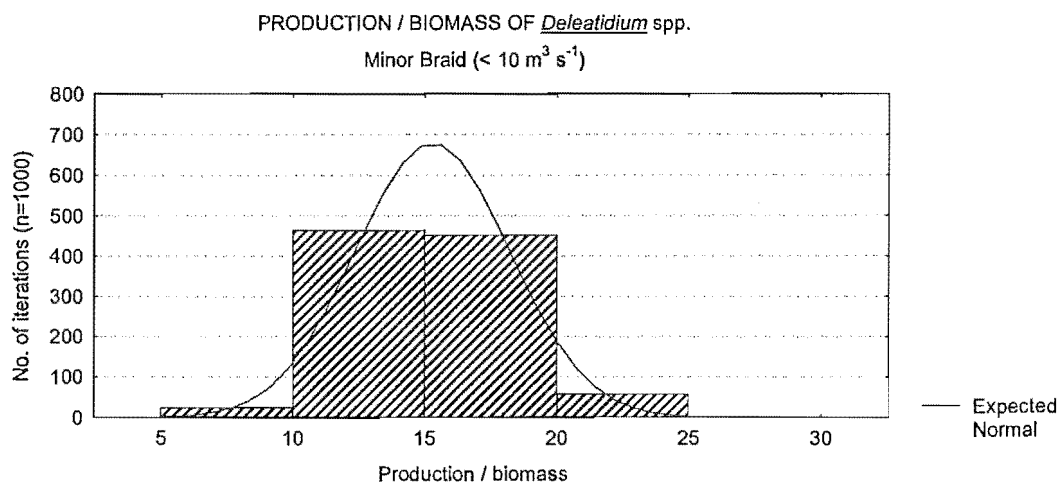
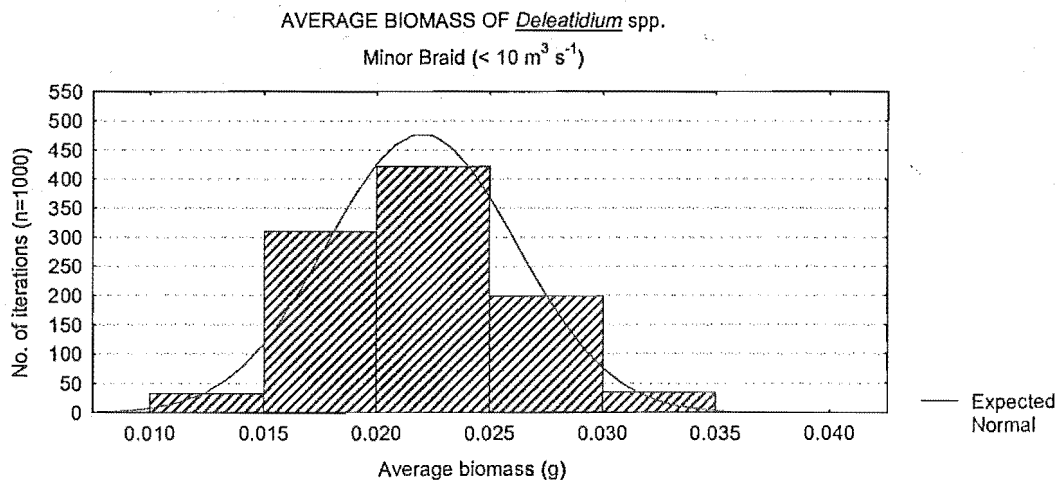
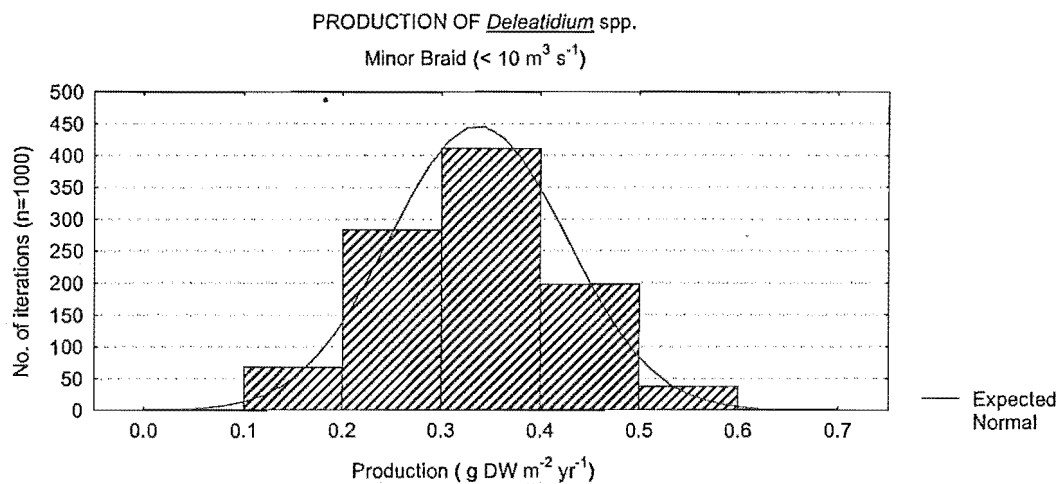




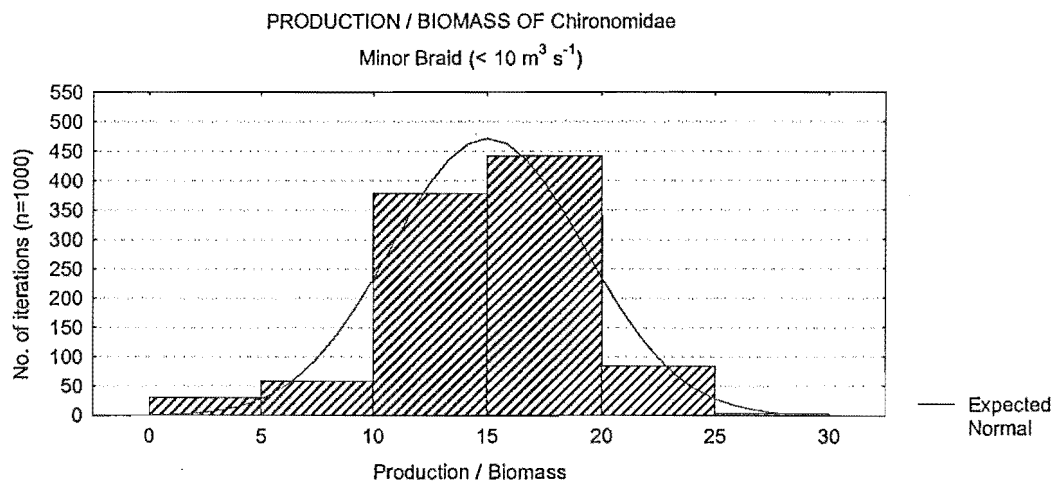
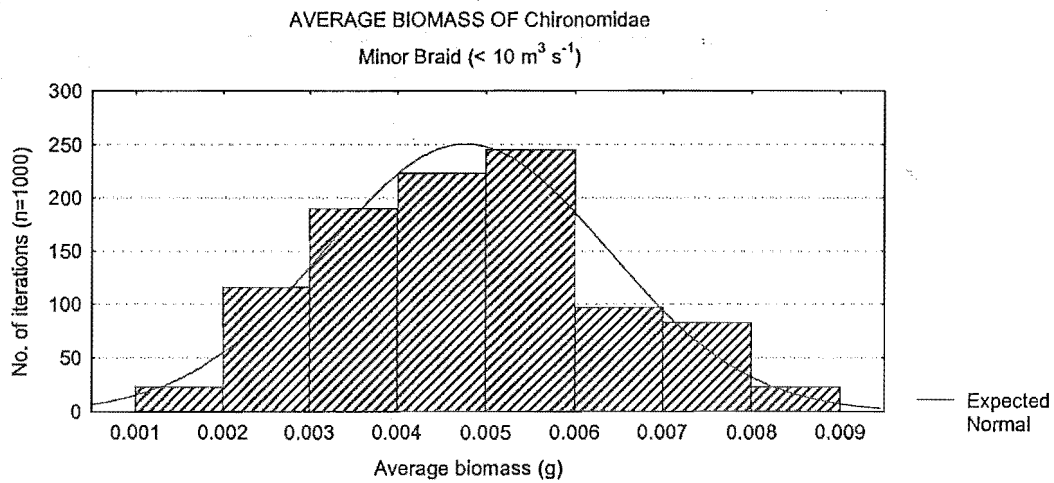
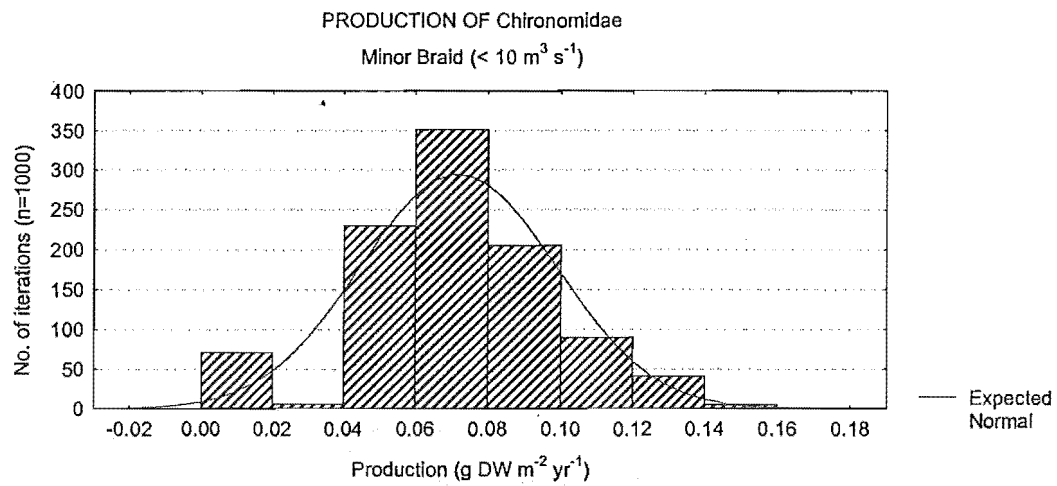


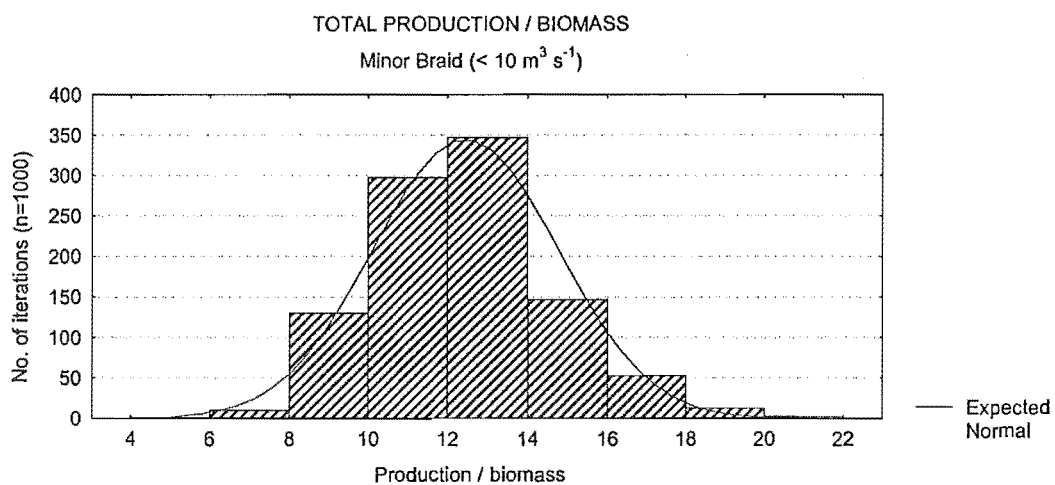
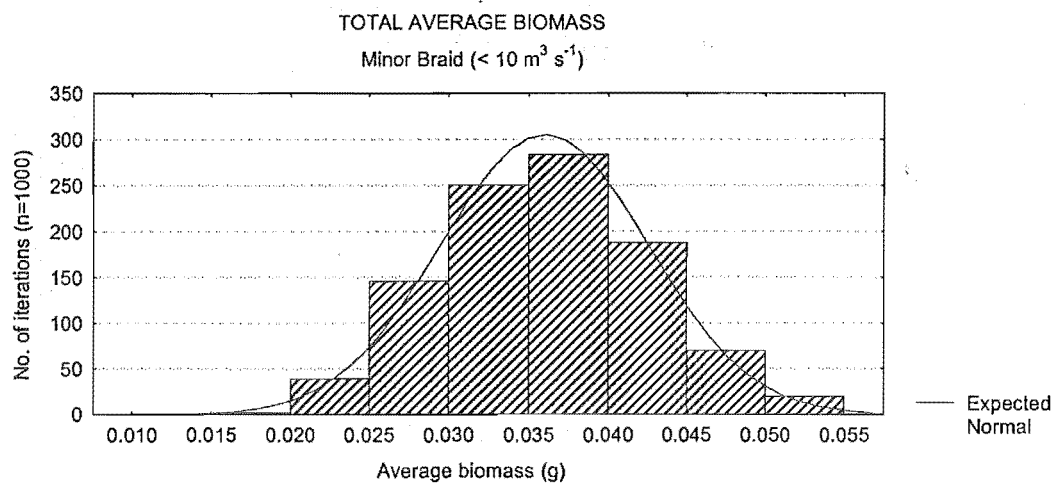
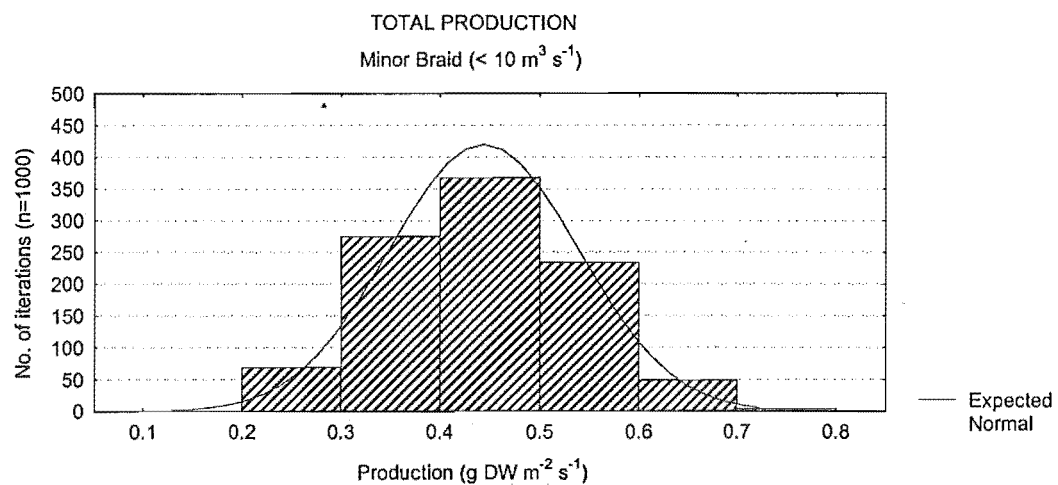


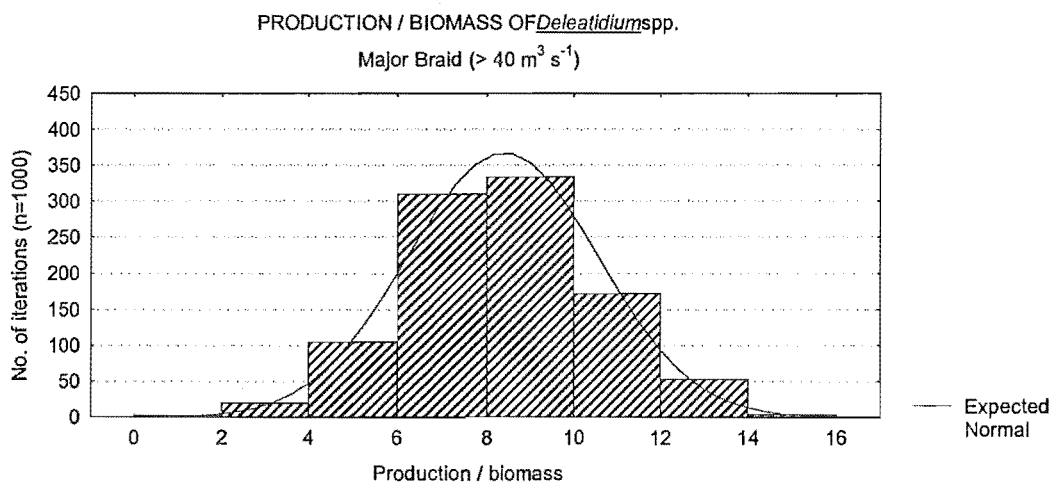
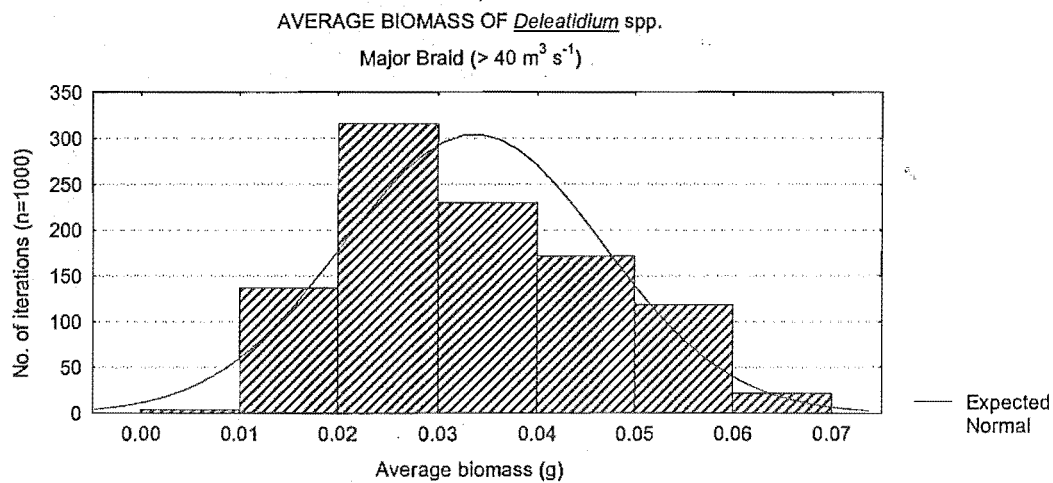
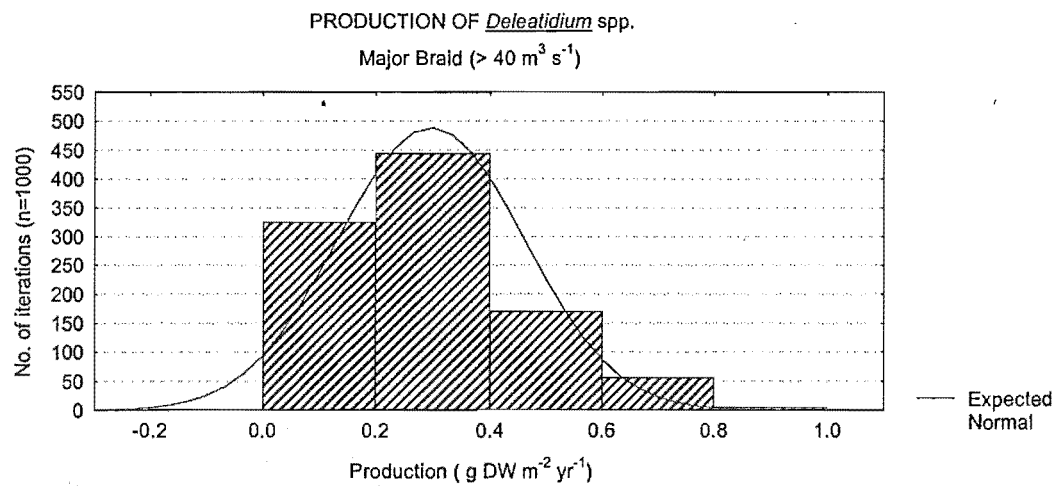


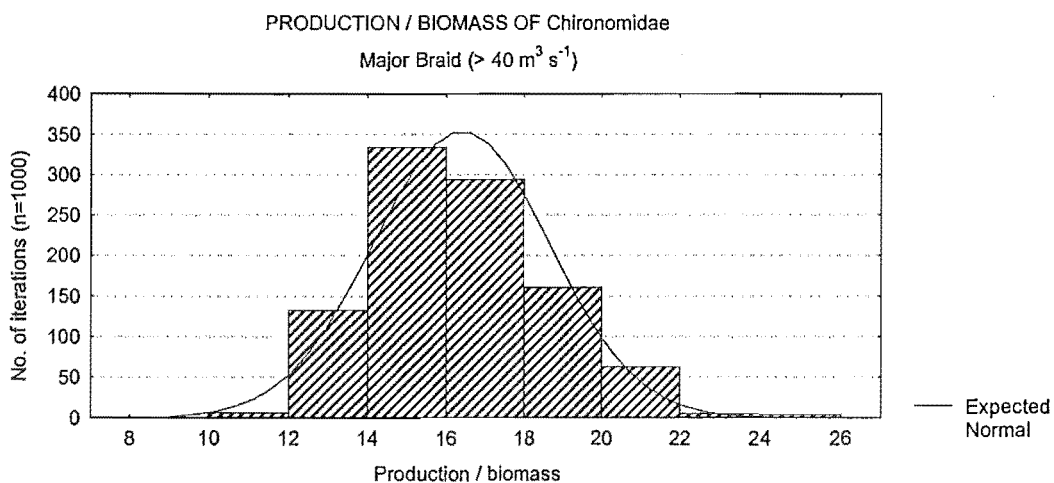
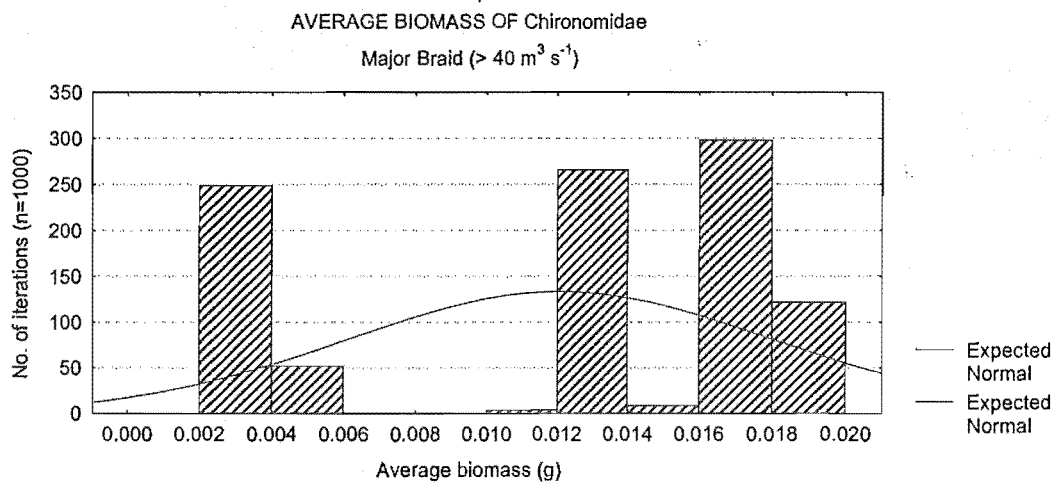
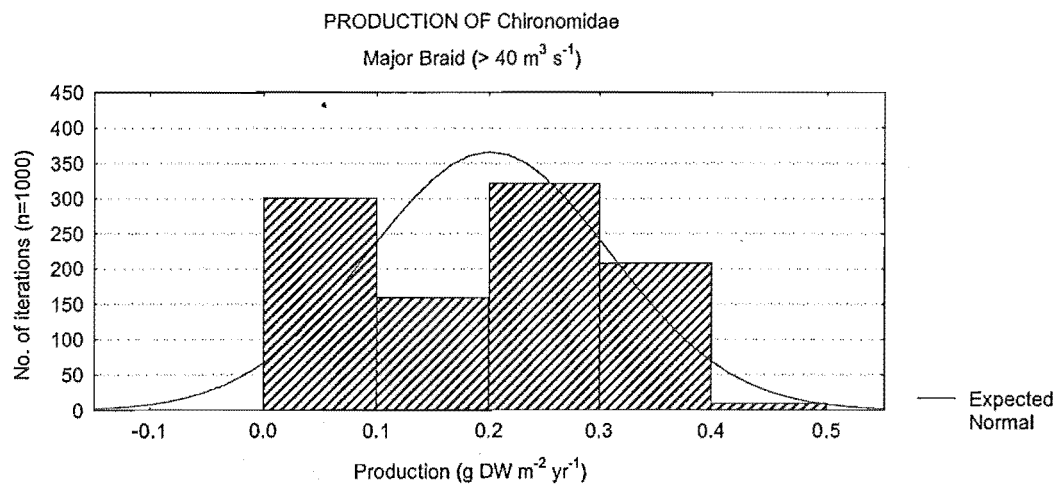


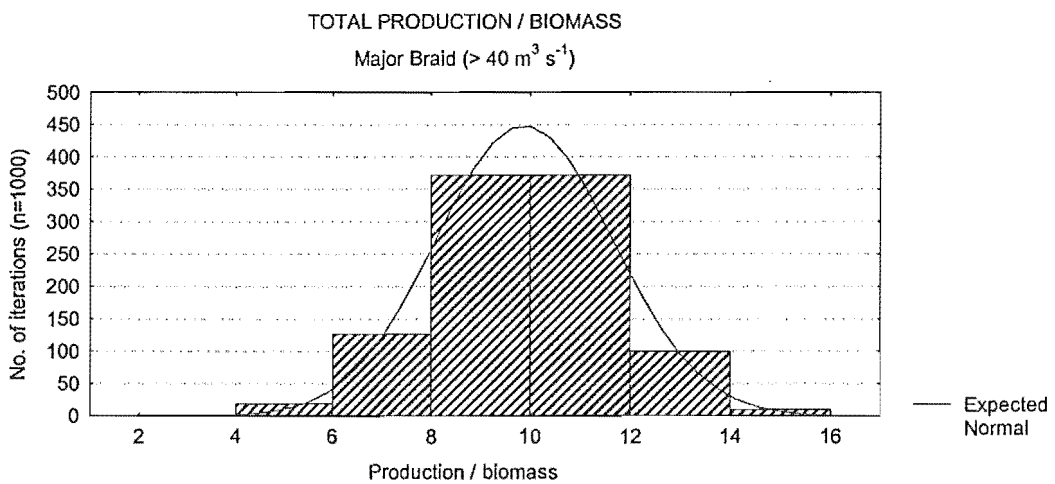
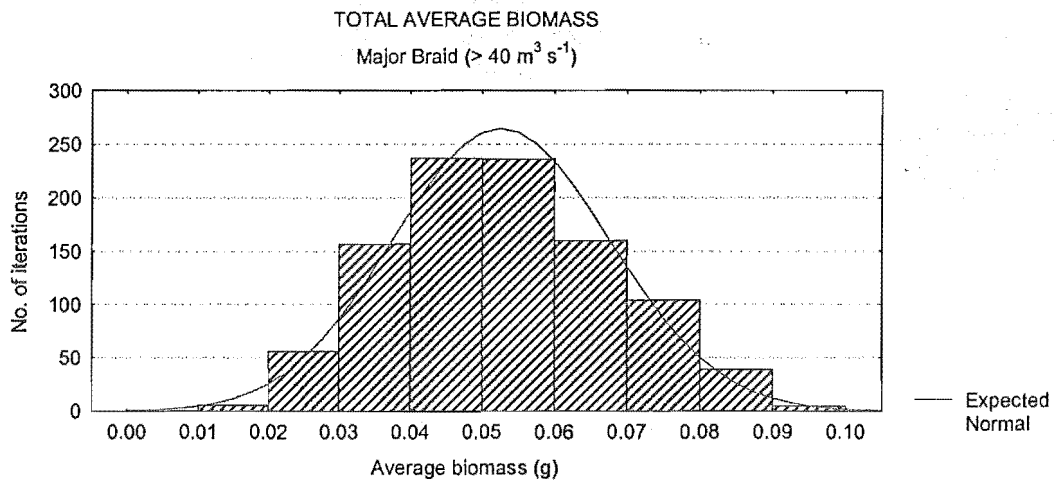
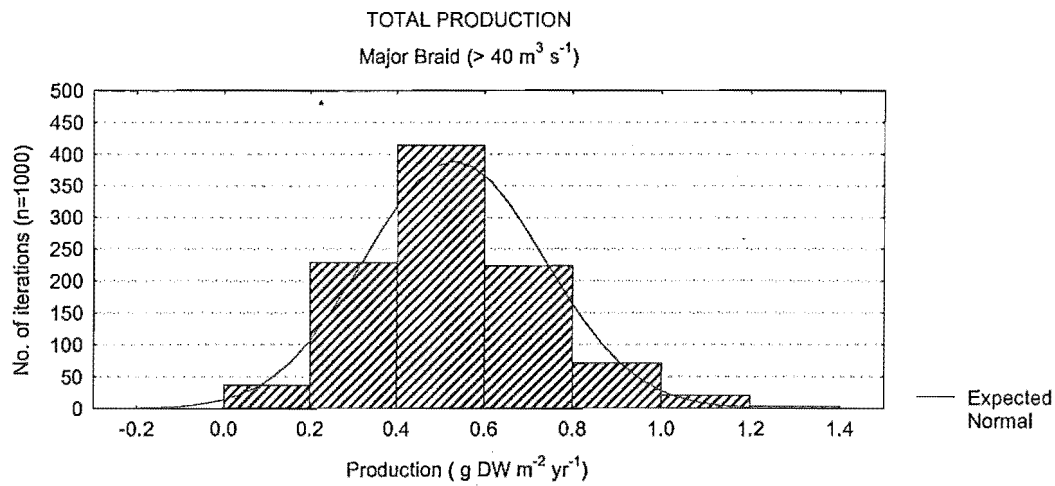














		VERTICAL HYDRAULIC GRADIENT					ALGAL ABUNDANCE RATING						
		PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR	MAJOR
16/10/97-22/10/97	1	0.13	0.11	0.00	-0.09	-0.11		5	4	1	1	1	
	2	0.12	0.07	0.04	-0.07	-0.13		5	4	1	1	1	
	3	0.13	0.13	0.03	-0.13	-0.10		5	4	1	1	1	
	4	0.10	0.03	0.05	-0.25	-0.07		5	4	1	1	1	
27/11/97-29/11/97	1	0.12	-0.01	0.01	-0.04	-0.11		5	3	1	1	3	
	2	0.05	0.02	0.03	-0.04	-0.24		5	3	1	1	3	
	3	0.02	0.01	0.05	-0.03	-0.03		5	3	1	1	3	
	4	0.04	-0.04	0.05	-0.20	-0.11		5	4	1	1	3	
10/1/98-4/3/98	1	0.11	0.04	0.05	-0.25	-0.18		4	1	1	3	4	
	2	0.03	0.05	0.06	-0.19	-0.21		4	1	1	3	4	
	3	-0.03	-0.01	0.08	-0.30	-0.30		4	1	1	3	4	
	4	-0.02	0.02	0.10	-0.26	-0.41		4	1	1	3	4	
18/4/98-23/4/98	1	0.18	0.17	0.42	-0.31	0.00		4	2	3	3	3	
	2	0.07	0.22	0.24	-0.17	-0.09		4	2	3	3	3	
	3	-0.17	0.14	0.24	-0.18	-0.09		4	2	3	3	3	
	4	-0.18	0.25	0.16	-0.34	-0.09		4	2	3	3	3	
18/5/98-25/5/98	1	0.10	0.34	-0.28	-0.13	-0.01		4	3	4	2	3	
	2	0.02	-0.32	-0.24	-0.15	-0.28		4	3	4	3	3	
	3	0.02	0.00	-0.33	-0.18	-0.30		5	3	4	4	3	
	4	-0.03	-0.11	-0.37	-0.18	-0.30		5	3	4	3	3	
30/6/98-5/7/98	1	0.11	-0.35	0.07	-0.01	-0.03		4	4	1	1	1	
	2	0.17	-0.25	0.08	-0.01	-0.06		4	4	1	1	1	
	3	0.19	-0.36	0.09	-0.09	-0.17		4	4	1	1	1	
	4	0.04	-0.43	0.10	-0.16	-0.28		4	4	1	1	1	
7/8/98-16/8/98	1	0.17	0.23	0.55	-0.14	-0.05		4	2	1	1	1	
	2	0.14	0.23	0.15	-0.13	-0.05		4	2	1	1	1	
	3	0.06	0.16	0.14	-0.19	-0.05		3	2	1	1	1	
	4	0.04	0.21	0.14	-0.06	0.04		3	2	1	1	1	

		COARSE PARTICULATE ORGANIC MATTER (g m <sup>-2</sup> )					FINE PARTICULATE ORGANIC MATTER (g m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR MAJOR	PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR MAJOR
16/10/97-22/10/97	1	2.36	0.50	0.12	0.30	1.05	11.43	0.51	0.31	0.35	0.41
	2	0.52	0.84	0.10	0.15	4.22	2.69	0.46	0.17	0.53	0.26
	3	0.58	0.39	0.11	0.15	0.10	3.16	1.09	0.38	0.63	0.39
	4	3.16	0.72	0.44	0.95	4.32	4.48	1.08	0.88	0.38	0.37
27/11/97-29/11/97	1	2.18	5.01	1.39	0.22	0.17	1.82	2.26	0.22	0.42	0.43
	2	2.59	1.46	4.29	0.46	0.20	2.96	1.30	0.94	0.42	0.43
	3	0.81	0.87	0.84	1.14	0.25	2.16	0.92	0.45	0.48	0.36
	4	1.21	5.55	1.54	0.16	0.39	1.52	1.86	0.67	0.32	0.46
10/1/98-4/3/98	1	4.32	0.58	0.28	0.11	3.97	2.74	1.79	0.40	0.40	1.37
	2	1.32	0.80	0.20	2.27	0.30	1.21	1.88	0.27	0.62	0.56
	3	0.42	1.18	0.12	0.52	0.27	1.07	2.36	0.39	0.37	0.37
	4	0.79	0.70	0.89	0.09	0.36	1.19	2.42	1.46	0.30	1.39
18/4/98-23/4/98	1	3.31	4.10	1.36	3.67	2.61	2.07	0.94	0.28	0.86	0.95
	2	5.08	0.64	2.14	1.77	1.17	2.76	0.46	0.47	0.75	1.74
	3	2.60	2.57	3.17	16.83	1.17	1.91	0.91	0.53	3.68	0.21
	4	1.00	0.71	1.11	1.70	1.36	0.58	0.35	0.36	0.55	0.44
18/5/98-25/5/98	1	1.50	0.05	3.96	0.21	0.86	18.56	0.60	1.87	0.72	1.31
	2	0.21	0.06	3.42	0.13	0.17	1.56	0.71	1.77	1.17	0.52
	3	0.62	0.11	0.30	0.30	0.31	34.11	0.54	1.40	1.05	1.32
	4	2.55	1.03	1.00	0.10	0.17	2.87	1.24	1.89	0.46	0.64
30/6/98-5/7/98	1	0.26	3.69	0.45	0.60	0.96	0.38	1.82	0.27	0.88	0.81
	2	0.46	0.54	0.03	0.10	0.50	0.66	0.69	0.29	0.29	0.76
	3	3.74	0.12	0.15	0.15	0.70	1.78	0.59	0.32	0.42	0.34
	4	3.27	0.44	0.01	0.01	1.36	2.63	1.20	0.23	0.15	0.65
7/8/98-16/8/98	1	0.75	2.12	2.78	2.49	0.87	2.10	1.89	2.33	0.90	0.73
	2	0.69	0.40	5.59	0.23	0.30	1.95	0.85	3.12	0.38	0.97
	3	1.27	0.98	3.62	0.42	5.75	1.18	0.90	1.85	0.51	1.16
	4	11.06	0.38	3.56	0.46	5.01	4.42	0.81	1.47	0.35	1.28



		SURFACE WATER CONDUCTIVITY ( $\mu\text{S cm}^{-1}$ )					INTERSTITIAL WATER CONDUCTIVITY ( $\mu\text{S cm}^{-1}$ )				
		PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR MAJOR	PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR MAJOR
16/10/97-22/10/97	1	60.5	57.1	66.4	62.5	63.3	65.6	60.2	72.2	67.2	60.6
	2	61	51.4	66.7	63.2	59.4	64.9	63.3	73.3	66.6	60.8
	3	61.1	58.6	66.8	63.3	58.3	67.1	64.1	73.8	67	60.2
	4	61.7	58.8	66.7	63.1	58.2	66.6	65.1	71.7	66.7	59.5
27/11/97-29/11/97	1	71.9	60	57.7	61.5	58.4	80	57.8	60.8	59.6	59.8
	2	69.7	59.9	57.5	61.5	58.3	74.5	59.5	60.8	59.9	60.7
	3	68.8	59.7	57.6	61.7	59.3	69.9	60	58.6	58.4	60.2
	4	68.1	59.6	57.8	62.4	57.9	64.5	60.5	58.6	59.1	61.6
10/1/98-4/3/98	1	73.7	59.8	60.2	56.4	62.6	77.1	61.3	63.9	57.5	63.7
	2	63.3	59.5	60.3	56	61.9	72.8	61.8	64.6	68.3	64.1
	3	63.4	59.8	60.1	56.5	62.9	65.8	61	61.8	57	63.1
	4	63.5	59.4	59.6	55.9	60.8	71.8	61.4	61.1	57.1	60.8
18/4/98-23/4/98	1	61.8	63.4	60.2	61.1	60.3	62.7	57.6	60.6	63.8	63.2
	2	60.6	55.8	59	61.2	61.4	63.8	57.9	59.7	62.2	64.4
	3	61.1	52.8	58.8	62.8	60.9	63	71	60.8	64.7	64.5
	4	61.2	56.6	59	61.6	61	64.3	61.2	60.7	64.5	64.4
18/5/98-25/5/98	1	60.8	59.1	62.5	57.8	58.6	67.8	57.9	65.4	58.7	55.8
	2	59.5	58.3	61.9	57.6	59.1	66.7	58.3	61.4	57	56.4
	3	59.3	57.9	62.1	58	59.4	65.6	58.1	64.1	57.6	58.2
	4	59.5	58.3	61.9	57.9	58.6	67.4	59.1	63.7	58	57.7
30/6/98-5/7/98	1	57.9	57.7	55.5	58.1	57.6	68.6	60.2	58	57.2	58
	2	57.7	57.9	56	58.2	57.7	69.5	60.1	56.2	57	56.4
	3	57.2	58	55.4	58.3	57.3	70.9	58.4	57.2	58	58.7
	4	57.1	57.8	56.9	55.8	55.8	69.2	58.8	58.7	58.4	58.6
7/8/98-16/8/98	1	58.1	56.1	59.5	60	59.8	68.9	58.8	61.3	60.4	63.4
	2	58.1	56.8	59.5	60	59.8	65.5	59	61.7	58.9	61.4
	3	58.6	56.5	59.7	60	59.4	66.4	61.1	64	60.7	61.6
	4	58.3	56.3	59.3	60	59.8	66.8	59.8	63.8	59.5	60.5

		INTERSTITIAL DISSOLVED OXYGEN (mg O <sub>2</sub> l <sup>-1</sup> )					SURFACE DISSOLVED OXYGEN (mg O <sub>2</sub> l <sup>-1</sup> )				
		PERENNIAL	BFSEEP	PAGE	BFS	SPRING MINOR MAJOR	PERENNIAL	BFSEEP	PAGE	BFS	SPRING MINOR MAJOR
16/10/97-22/10/97	1	8.9	7.8	8.3	9.1	9.4	10.2	8.1	9	9.9	10.3
	2	9	7.8	7.4	9.5	8.5	9.4	7.9	9	9.7	10.4
	3	8.5	7.8	8.5	9.4	9.4	10.2	9	9.1	9.7	10.3
	4	7.9	5.8	8.1	9.4	9.9	10.2	8.5	9.4	9.9	10.2
27/11/97-29/11/97	1	5.5	8.2	7.9	9	9	9.5	9.1	9.2	8.9	9.3
	2	7.2	8	7.9	7.1	9.2	9.2	8.9	9.2	8.3	9.4
	3	7.7	8	8.9	8.8	8.5	9.2	8.5	9.2	9	9.4
	4		8.8	8.9	9.3	9	9.3	8.5	9.2	8.6	9.2
10/1/98-4/3/98	1	5.7	8	8.1	9	9.6	9	8.8	9	9.5	9.7
	2	5.8	8	7.9	8.8	9.6	8.8	8.7	9	9.4	9.8
	3	8.1	7.9	8.7	8.7	9.4	8.7	8.7	8.9	9.5	9.6
	4	7.2	7.9	8.7	9.5	9.8	8.8	8.7	8.8	9.6	9.9
18/4/98-23/4/98	1	8.4	9.2	8.8	8.4	8.4	10.4	10.2	8.9	10	9.6
	2	8.2	9	8.7	8.9	8.45	10	9.8	9.2	10	9.5
	3	8.3	8.5	8.2	8.4	7.7	10.6	9.8	9.2	10.2	9.5
	4	9.4	8.1	8	8	7.7	10	9.6	9.2	9.7	9.5
18/5/98-25/5/98	1	6.6	9.5	9.1	9.7	8.5	9.9	10.1	10.4	10.3	10.1
	2	7	9.2	9.7	9.7	9.5	9.8	10.4	10.2	10.2	10
	3	7.1	10.2	9	9.8	8.7	9.8	10.3	10.1	10.3	10
	4	7.2	9.8	8.8	9.9	8.9	10	10.4	10.3	10.2	10
30/6/98-5/7/98	1	7.8	9.1	9.8	9.8	10.4	9.6	10	9.8	9.7	9.6
	2	7.4	9.6	9.8	9.9	10.3	9.5	9.9	9.8	9.7	9.8
	3	7.2	10	9.6	9.5	10	9.9	10.1	9.9	9.9	9.6
	4	7.5	9.9	9.8	10	10	9.8	10.2	9.8	9.8	9.7
7/8/98-16/8/98	1	7.3	9.4	10.1	10	10.3	9.8	9.9	9.8	9.8	10.2
	2	8.2	9.3	9.7	10.2	10.3	9.6	9.5	9.8	9.8	10.1
	3	8.1	9.2	9.5	10.3	10.3	10.2	9.7	9.9	9.8	10.2
	4	8	9.1	9.5	10.3	10	10.2	9.7	9.9	9.8	10

		SURFACE WATER TEMPERATURE (°C)						INTERSTITIAL WATER TEMPERATURE (°C)									
		PERENNIAL	BFSEEP	PAGE	BFS	SPRING	MINOR	MAJOR	PERENNIAL	BFSEEP	PAGE	BFS	SPRING	MINOR	MAJOR		
16/10/97-22/10/97	1	14		17		12		17	12	10		13		11		16	11
	2	14		20		12		18	12	15		17		11		16	12
	3	15		20		13		18	12	11		14		11		16	11
	4	14		21		12		17	12	11		15		11		17	11
27/11/97-29/11/97	1	16		16		15		15	15	13		14		14.5		15	15
	2	17		15		15		15	15	13		15		14.5		15	15
	3	16		16		15		15	15	14		15		14.5		15	15
	4	14		16		15		15	15	14		15		14.5		15	15
10/1/98-4/3/98	1	20		19		17		18.5	17	16		17		16		18	17
	2	20.5		19		16		18.5	17	17		17		15		18	17
	3	22.5		19		16		18.5	17	19		17		15		18	18
	4	22		19		17		18.5	18	18		17		16		18	18
18/4/98-23/4/98	1	12		12		13		11	12	12		12		13		11	12
	2	12		11		13.5		10.5	12	12		12		13.5		10.5	12
	3	12		11		14		10	12	12		12		13.5		10	12
	4	13		12		14		10	12	12		12		13.5		10	12
18/5/98-25/5/98	1	9		10		13.5		9.5	12	13		11		12		10	12
	2	9		10.5		14		9.5	12	13		11		12		10	12
	3	9.5		10.5		14		9.5	12	11.5		11		12.5		10	12
	4	10		11		15		9.5	12	11		11		12.5		10	12
30/6/98-5/7/98	1	8		8.5		8		7.5	7.5	9		8.5		8.5		7.5	7.5
	2	8		8.5		8		8	7.5	9		8.5		8.5		8	7.5
	3	8.5		8.5		8		7.5	8	9		8.5		8.5		7.5	8
	4	8		8.5		8.5		7.5	8	9		8.5		8.5		7.5	8
7/8/98-16/8/98	1	10.5		9		7.5		8.5	7	9.5		9		8		8.5	6
	2	10.5		9		7		8.5	6.5	9.5		9		8		7.5	6
	3	10		9.5		7		8.5	7	9.5		9.5		8		7.5	6.5
	4	9		10		7		8.5	6	9		9		8		7.5	6.5

		SILT DEPOSITED WITHIN THE BED (g 0.1 m <sup>-3</sup> )				
		PERENNIAL	BFSEEPAGE	BFS	SPRING	MINOR MAJOR
16/10/97-22/10/97	1	322	192	4	3	4
	2	600	868	0	14	62
	3	156	866	8	0	5
	4	401	402	0	5	50
27/11/97-29/11/97	1	1207	58	291	120	57
	2	1400	39	340	543	129
	3	1753	87	673	170	422
	4	1737	237	456	472	290
10/1/98-4/3/98	1	2443	2324	362	210	444
	2	1451	2343	516	348	657
	3	2933	2771	189	273	1155
	4	2009	3665	1200	716	680
18/4/98-23/4/98	1	1153	1255	2214	1120	611
	2	1656	1372	1095	1178	795
	3	883	1357	1079	1033	0
	4	1299	1361	1744	1679	0
18/5/98-25/5/98	1	1843	1316	0	920	0
	2	592	3059	0	990	0
	3	1588	254	0	558	0
	4	1115	1970	0	958	980
30/6/98-5/7/98	1	1743	765	2408	822	0
	2	1700	1981	1011	952	0
	3	1026	2984	1534	820	462
	4	1060	1746	2500	483	224
7/8/98-16/8/98	1	1184	1732	62	952	1036
	2	3498	4851	150	1014	999
	3	3653	1984	300	2113	1264
	4	2325	2405	140	621	797

		RELATIVE PRODUCTION					TOTAL DRY WEIGHT (g m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	6.66	29.76	9.49	7.54	2.81	0.72	2.28	0.68	0.54	0.20
	2	15.61	32.90	3.11	4.22	5.16	1.48	2.17	0.22	0.30	0.37
	3	10.77	33.76	13.71	6.53	0.02	1.05	2.42	0.98	0.48	0.00
	4	15.01	41.20	16.96	4.22	3.88	1.75	2.91	1.21	0.29	0.27
27/11/97-29/1	1	26.19	0.43	2.80	2.18	1.89	4.01	0.03	0.20	0.16	0.13
	2	19.97	1.32	7.03	1.09	0.99	3.21	0.09	0.51	0.08	0.07
	3	10.62	1.70	5.30	3.64	2.57	1.01	0.35	0.38	0.29	0.19
	4	14.26	3.52	2.81	1.88	6.21	1.84	0.24	0.20	0.14	0.45
10/1/98-4/3/98	1	49.89	32.41	5.63	4.10	12.22	3.18	2.32	0.41	0.24	0.68
	2	23.67	19.76	2.53	4.04	8.64	1.81	1.41	0.18	0.25	0.50
	3	31.22	32.01	5.83	6.56	3.22	2.16	2.29	0.41	0.43	0.21
	4	25.50	27.90	11.95	4.25	12.25	1.92	2.02	0.82	0.30	0.68
18/4/98-23/4/98	1	51.54	7.95	5.94	4.78	0.00	3.27	0.55	0.42	0.33	0.00
	2	68.72	7.12	6.18	2.09	0.06	4.18	0.50	0.44	0.15	0.01
	3	45.17	10.17	6.77	4.84	0.47	2.83	0.71	0.49	0.33	0.03
	4	29.70	4.19	11.13	2.80	0.00	1.75	0.29	0.81	0.19	0.00
18/5/98-25/5/98	1	50.82	15.96	16.64	0.86	0.47	3.29	1.03	1.08	0.06	0.03
	2	34.39	26.04	11.24	2.71	0.32	2.33	1.66	0.70	0.14	0.02
	3	52.21	40.16	12.30	2.95	0.61	3.29	2.72	0.70	0.17	0.04
	4	56.57	26.80	16.83	0.08	0.02	3.45	1.52	0.96	0.00	0.00
30/6/98-5/7/98	1	19.91	24.04	12.44	2.72	0.45	1.75	1.37	0.85	0.19	0.03
	2	26.28	17.38	15.98	0.19	0.52	2.72	1.05	1.08	0.01	0.03
	3	42.33	10.95	19.24	0.77	0.17	3.22	0.67	1.27	0.05	0.01
	4	93.27	15.38	10.87	0.49	1.18	7.93	0.97	0.77	0.03	0.07
7/8/98-16/8/98	1	41.28	27.68	2.48	1.90	1.03	2.85	1.96	0.17	0.13	0.06
	2	42.55	26.39	12.26	1.09	1.76	3.04	1.90	0.84	0.08	0.12
	3	31.31	28.47	2.37	1.22	9.07	2.50	2.10	0.13	0.08	0.64
	4	115.36	28.27	18.40	5.45	9.54	6.86	2.07	1.31	0.39	0.67

		TOTAL INVERTEBRATE DENSITIES (No. m <sup>-2</sup> )					CHIRONOMIDAE DENSITY (No. m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	5311	8789	778	1133	300	3511	6722	33	478	78
	2	5322	6633	278	578	244	3300	3789	0	178	178
	3	5033	6678	1056	1033	500	2856	3256	44	344	0
	4	7689	4878	1267	1111	578	3189	1700	22	389	233
27/11/97-29/1	1	6200	1033	222	178	233	2500	967	0	22	78
	2	6133	2100	467	78	167	2344	1933	0	0	89
	3	11556	244	456	289	333	9222	211	0	11	133
	4	6000	3978	222	189	733	3000	5078	11	44	244
10/1/98-4/3/98	1	9444	2600	444	556	1344	6411	22	22	400	1011
	2	6033	1456	233	600	1544	2189	0	11	422	1044
	3	4044	2667	444	589	467	1800	22	33	233	244
	4	6244	2111	956	400	1967	2844	0	189	144	1567
18/4/98-23/4/98	1	4078	800	1311	411	111	1811	67	0	22	0
	2	6144	667	589	189	233	2789	44	0	11	0
	3	4656	978	533	578	278	2789	33	11	67	0
	4	3000	589	844	333	156	1956	0	0	33	0
18/5/98-25/5/98	1	8200	2100	1789	122	89	5344	1089	733	67	0
	2	5956	3311	1267	178	67	4544	1867	511	167	0
	3	9478	3833	1689	267	78	7089	1933	1189	78	33
	4	9944	5344	2367	44	11	7567	4189	1589	11	0
30/6/98-5/7/98	1	4389	5589	1356	233	89	2789	4867	444	44	56
	2	9933	4522	2111	44	89	8233	3844	733	22	44
	3	16311	3111	3589	100	22	13122	2556	2033	22	0
	4	20667	3767	1011	56	178	14189	2833	211	11	100
7/8/98-16/8/98	1	82311	1522	244	144	133	27822	200	0	11	78
	2	17722	1256	400	100	178	15378	33	0	0	67
	3	4033	1456	278	111	311	2389	44	0	33	0
	4	4489	1467	644	233	311	52533	33	0	0	0

		DENSITY OF <i>Deleatidium</i> (No. m <sup>-2</sup> )					DENSITY OF EARLY INSTAR <i>Deleatidium</i> (No. m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	267	1756	678	533	200	22	133	211	67	11
	2	956	1800	222	300	367	22	200	0	44	56
	3	578	2400	989	467	211	78	178	89	78	0
	4	589	2867	1333	289	267	56	522	56	0	11
27/11/97-29/1	1	656	22	200	156	133	33	0	56	0	11
	2	411	78	500	78	67	56	0	11	0	22
	3	467	0	378	222	178	33	0	56	0	0
	4	556	200	200	133	433	22	11	0	33	33
10/1/98-4/3/9	1	878	2533	389	100	200	422	1644	278	33	67
	2	611	1422	178	89	167	322	711	100	33	22
	3	1456	2189	389	311	0	956	1511	311	100	78
	4	667	2011	756	200	222	522	900	389	56	144
18/4/98-23/4/	1	1833	511	422	311	11	511	178	278	122	0
	2	1900	456	444	0	0	600	111	211	11	0
	3	756	667	478	311	33	133	122	244	44	0
	4	200	289	789	178	0	44	122	456	67	0
18/5/98-25/5/	1	1533	756	833	44	33	844	456	544	11	0
	2	589	1111	500	11	11	433	756	322	0	0
	3	622	1933	289	100	22	389	1600	178	89	0
	4	1044	456	400	0	0	633	211	233	0	0
30/6/98-5/7/9	1	789	456	767	133	22	456	56	489	144	11
	2	789	589	1011	11	22	433	222	711	11	11
	3	1489	400	1067	44	11	678	167	833	44	0
	4	4300	622	767	33	56	1356	267	644	22	22
7/8/98-16/8/9	1	878	1211	156	133	44	222	544	44	22	0
	2	1544	1144	333	78	100	822	489	211	11	33
	3	1222	1311	144	78	278	789	589	78	44	67
	4	3289	1422	444	222	278	1389	611	289	100	56

		<i>Deleatidium</i> DW (g m <sup>-2</sup> )					CHIRONOMIDAE DW (g m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	0.28	1.88	0.68	0.53	0.20	0.03	0.09	0.00	0.00	0.00
	2	0.90	1.81	0.22	0.30	0.37	0.02	0.28	0.00	0.00	0.00
	3	0.59	2.29	0.98	0.46	0.00	0.02	0.04	0.00	0.00	0.00
	4	0.64	2.88	1.21	0.29	0.27	0.03	0.01	0.00	0.00	0.01
27/11/97-29/1	1	0.66	0.02	0.20	0.16	0.13	0.07	0.00	0.00	0.00	0.00
	2	0.36	0.08	0.50	0.08	0.07	0.08	0.01	0.00	0.00	0.00
	3	0.46	0.00	0.38	0.22	0.18	0.08	0.00	0.00	0.00	0.00
	4	0.53	0.20	0.20	0.13	0.43	0.03	0.03	0.00	0.00	0.01
10/1/98-4/3/9	1	0.89	2.29	0.39	0.10	0.20	1.71	0.02	0.00	0.13	0.47
	2	0.62	1.41	0.18	0.09	0.17	0.57	0.00	0.00	0.13	0.31
	3	1.46	2.21	0.41	0.31	0.12	0.48	0.05	0.00	0.11	0.07
	4	0.67	1.98	0.74	0.20	0.20	0.62	0.00	0.08	0.06	0.47
18/4/98-23/4/	1	1.81	0.51	0.42	0.31	0.00	1.23	0.03	0.00	0.02	0.00
	2	1.87	0.46	0.43	0.14	0.00	2.03	0.03	0.00	0.00	0.00
	3	0.77	0.67	0.48	0.31	0.03	1.55	0.03	0.00	0.02	0.00
	4	0.44	0.29	0.79	0.17	0.00	1.07	0.00	0.00	0.02	0.00
18/5/98-25/5/	1	1.56	0.76	0.83	0.04	0.03	1.33	0.27	0.25	0.01	0.00
	2	0.60	1.14	0.49	0.01	0.02	1.09	0.50	0.20	0.13	0.00
	3	0.64	2.17	0.29	0.10	0.02	1.96	0.48	0.41	0.07	0.01
	4	1.04	0.46	0.40	0.00	0.00	1.98	1.01	0.55	0.00	0.00
30/6/98-5/7/9	1	0.82	0.47	0.77	0.17	0.02	0.24	0.87	0.07	0.01	0.01
	2	0.79	0.59	0.98	0.01	0.02	0.41	0.45	0.10	0.00	0.01
	3	1.48	0.40	1.07	0.04	0.01	0.87	0.27	0.19	0.01	0.00
	4	4.40	0.63	0.74	0.03	0.04	0.88	0.32	0.02	0.00	0.02
7/8/98-16/8/9	1	0.99	1.93	0.17	0.13	0.04	1.24	0.02	0.00	0.00	0.02
	2	2.20	1.87	0.84	0.08	0.10	0.51	0.01	0.00	0.00	0.02
	3	1.94	2.00	0.13	0.08	0.64	0.11	0.00	0.00	0.01	0.00
	4	3.36	1.99	1.29	0.39	0.67	3.31	0.01	0.00	0.00	0.00



		<u><i>Aoteapsyche</i> spp. DW (g m<sup>-2</sup>)</u>					<u>HYDROBIOSIDAE DW (g m<sup>-2</sup>)</u>				
		PERENNIAL	BFSEEPAGE	BFS	SPRING MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFS	SPRING MINOR	MAJOR
16/10/97-22/1	1	0.18	0.17	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00
	2	0.20	0.02	0.00	0.00	0.00	0.06	0.04	0.00	0.00	0.00
	3	0.04	0.00	0.00	0.00	0.00	0.04	0.03	0.00	0.02	0.00
	4	0.22	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
27/11/97-29/1	1	2.31	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
	2	1.94	0.00	0.00	0.00	0.00	0.07	0.00	0.01	0.00	0.00
	3	0.08	0.00	0.00	0.00	0.00	0.08	0.02	0.00	0.00	0.01
	4	0.54	0.00	0.00	0.00	0.00	0.08	0.01	0.00	0.00	0.01
10/1/98-4/3/98	1	0.32	0.00	0.02	0.00	0.00	0.06	0.01	0.00	0.00	0.01
	2	0.28	0.00	0.00	0.00	0.02	0.03	0.00	0.00	0.02	0.01
	3	0.13	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.00	0.00
	4	0.36	0.00	0.00	0.04	0.00	0.03	0.03	0.00	0.00	0.00
18/4/98-23/4/98	1	0.02	0.00	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.00
	2	0.04	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.00	0.01
	3	0.10	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00
	4	0.05	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.00	0.00
18/5/98-25/5/98	1	0.29	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.00	0.00
	2	0.55	0.00	0.00	0.00	0.00	0.02	0.01	0.02	0.00	0.00
	3	0.49	0.00	0.00	0.00	0.00	0.03	0.08	0.00	0.00	0.00
	4	0.34	0.00	0.00	0.00	0.00	0.03	0.06	0.01	0.00	0.00
30/6/98-5/7/98	1	0.53	0.00	0.00	0.00	0.00	0.05	0.03	0.01	0.01	0.00
	2	1.42	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
	3	0.75	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.00
	4	2.27	0.00	0.00	0.00	0.00	0.07	0.02	0.00	0.00	0.00
7/8/98-16/8/98	1	0.42	0.00	0.00	0.00	0.00	0.09	0.01	0.00	0.00	0.00
	2	0.12	0.00	0.00	0.00	0.00	0.10	0.02	0.00	0.00	0.00
	3	0.25	0.00	0.00	0.00	0.00	0.16	0.09	0.00	0.00	0.00
	4	0.06	0.00	0.00	0.00	0.00	0.08	0.07	0.02	0.00	0.00

		<u><i>Pycnocentroides aureola</i></u> DW (g m <sup>-2</sup> )					<u><i>Zelandobius furcillatus</i></u> (g m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR	PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	0.15	0.13	0.00	0.00	0.00	0.01	0.03	0.00	0.00	0.00
	2	0.30	0.01	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00
	3	0.34	0.05	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
	4	0.76	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.01	0.00
27/11/97-29/1	1	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	3	0.16	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	4	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10/1/98-4/3/9.	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	3	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18/4/98-23/4/	1	0.02	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.00
	2	0.03	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00
	3	0.08	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.02	0.00
	4	0.00	0.00	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.00
18/5/98-25/5/	1	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.03	0.00	0.00
	3	0.05	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.01	0.00
	4	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.02	0.00	0.00
30/6/98-5/7/9.	1	0.06	0.00	0.00	0.00	0.00	0.05	0.01	0.02	0.01	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.00
	3	0.05	0.00	0.00	0.00	0.00	0.02	0.00	0.05	0.00	0.00
	4	0.09	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.01
7/8/98-16/8/9.	1	0.02	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.00	0.00
	2	0.02	0.00	0.00	0.00	0.00	0.03	0.00	0.04	0.00	0.00
	3	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.05	0.00	0.00
	4	0.02	0.00	0.00	0.00	0.00	0.14	0.00	0.03	0.00	0.02

		ELMIDAE DW (g m <sup>-2</sup> )				
		PERENNIAL	BFSEEPAGE	BFSRING	MINOR	MAJOR
16/10/97-22/1	1	0.07	0.01	0.00	0.00	0.00
	2	0.00	0.01	0.00	0.00	0.00
	3	0.02	0.01	0.00	0.00	0.00
	4	0.07	0.02	0.00	0.00	0.00
27/11/97-29/1	1	0.18	0.00	0.00	0.00	0.00
	2	0.17	0.00	0.00	0.00	0.00
	3	0.15	0.00	0.00	0.07	0.00
	4	0.09	0.00	0.00	0.00	0.00
10/1/98-4/3/9:	1	0.16	0.00	0.00	0.01	0.01
	2	0.20	0.00	0.00	0.01	0.00
	3	0.05	0.00	0.00	0.00	0.00
	4	0.24	0.01	0.00	0.00	0.00
18/4/98-23/4/!	1	0.15	0.00	0.00	0.00	0.00
	2	0.18	0.02	0.01	0.00	0.00
	3	0.28	0.01	0.00	0.00	0.00
	4	0.16	0.00	0.00	0.00	0.00
18/5/98-25/5/!	1	0.06	0.00	0.00	0.00	0.00
	2	0.06	0.00	0.00	0.00	0.00
	3	0.12	0.00	0.00	0.00	0.00
	4	0.05	0.00	0.00	0.00	0.00
30/6/98-5/7/9:	1	0.01	0.00	0.00	0.00	0.00
	2	0.01	0.00	0.00	0.00	0.00
	3	0.01	0.00	0.00	0.00	0.00
	4	0.19	0.00	0.00	0.00	0.00
7/8/98-16/8/9:	1	0.00	0.00	0.00	0.00	0.00
	2	0.01	0.00	0.00	0.00	0.00
	3	0.00	0.00	0.00	0.00	0.00
	4	0.00	0.00	0.00	0.00	0.00

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
Size Class		1, 21/10/97	2, 21/10/97	3, 21/10/97	4, 21/10/97	1, 16/10/97	2, 16/10/97	3, 16/10/97	4, 16/10/97	1, 22/10/97	2, 22/10/97	3, 22/10/97	4, 22/10/97
Small cobble	128 mm - 64 mm	544.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	369.29	535.05	524.05	443.05	202.33	658.36	103.50	309.69	0.00	550.91	415.12	821.93
Coarse gravel	32 mm - 16 mm	336.48	341.82	345.28	517.00	613.43	276.20	427.81	404.02	802.35	455.84	433.16	379.58
Medium gravel	16 mm - 8 mm	417.70	117.91	135.21	49.60	318.52	302.04	255.68	423.05	320.79	166.96	124.60	128.13
Fine gravel	8 mm - 4 mm	285.32	202.37	125.99	206.66	408.48	449.56	484.52	492.38	188.99	166.49	142.24	23.60
Very fine gravel	4 mm - 2 mm	158.52	131.67	56.43	138.27	151.10	162.93	234.66	242.92	34.72	41.25	46.89	0.00
Very coarse sand	2 mm - 1 mm	120.46	90.52	30.27	99.87	47.17	52.32	45.14	104.69	12.47	4.99	25.69	0.00
Coarse sand	1 mm - 0.5 mm	64.59	36.21	13.18	37.50	18.44	19.55	9.86	49.76	1.06	0.38	8.11	0.00
Medium sand	0.5 mm - 0.25 mm	61.81	19.82	7.22	33.12	25.05	18.79	19.91	42.55	0.73	0.05	5.97	0.00
Fine sand	0.25 mm - 0.125 mm	225.04	81.17	23.23	108.13	62.19	54.61	102.63	62.26	0.68	0.26	6.55	0.00
Very fine sand	0.125 mm - 0.063 mm	83.91	55.62	19.20	50.63	32.87	30.26	59.82	33.91	0.30	0.21	2.32	0.00
Silt	< 0.063 mm	9.55	7.23	4.26	10.41	6.71	12.68	12.43	8.35	0.08	0.00	0.21	0.00
<b>Visual assessment of surface composition</b>													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	0%	0%	0%	4%	0%	0%	1%	1%	1%	0%
% Small gravel.	(2-32)	38%	16%	12%	10%	24%	47%	71%	18%	66%	40%	23%	15%
% Large gravel.	(32-64)	13%	50%	35%	34%	13%	2%	2%	47%	22%	0%	69%	45%
% Small cobbles.	(64-128)	49%	23%	19%	31%	21%	25%	9%	7%	10%	22%	7%	25%
% Large cobbles.	(128-256)	0%	12%	34%	24%	42%	23%	17%	28%	0%	22%	0%	15%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%	0%	15%	0%	0%
<b>bed composition (g)</b>													
		Minor				Major							
Size Class		1, 22/10/97	2, 22/10/97	3, 22/10/97	4, 22/10/97	1, 20/10/97	2, 20/10/97	3, 20/10/97	4, 20/10/97	1, 20/10/97	2, 20/10/97	3, 20/10/97	4, 20/10/97
Small cobble	128 mm - 64 mm	0	0	0	0	0	0	0	0	0	0	0	0
Very coarse gravel	64 mm - 32 mm	1000	257.97	172.62	821.8	694.7	429.94	597.48	475.83				
Coarse gravel	32 mm - 16 mm	454.02	554.49	773.86	249.15	629.79	697.53	255.25	468.49				
Medium gravel	16 mm - 8 mm	75.31	174.878	215.58	204.526	100.48	177.811	124.287	304.095				
Fine gravel	8 mm - 4 mm	100.973	390.464	145.983	187.171	240.673	416.633	191.701	328.752				
Very fine gravel	4 mm - 2 mm	21.432	173.492	53.461	51.723	143.403	228.994	80.269	138.866				
Very coarse sand	2 mm - 1 mm	2.283	100.47	30.67	17.834	56.239	137.799	37.952	107.62				
Coarse sand	1 mm - 0.5 mm	0.175	25.193	5.868	4.23	17.188	34.682	13.215	60.03				
Medium sand	0.5 mm - 0.25 mm	0.155	8.971	3.477	1.708	49.43	54.22	10.764	125.65				
Fine sand	0.25 mm - 0.125 mm	0.426	10.26	6.273	2.556	50.98	110.66	21.293	146.44				
Very fine sand	0.125 mm - 0.063 mm	0.221	5.631	4.54	1.426	19.214	42.72	7.702	47.4				
Silt	< 0.063 mm	0.064	0.56	0.97	0.096	0.407	4.036	0.15	2.639				
<b>Visual assessment of surface composition</b>													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%				
% Small gravel.	(2-32)	17%	11%	0%	0%	45%	45%	50%	15%				
% Large gravel.	(32-64)	34%	42%	11%	11%	2%	2%	17%	15%				
% Small cobbles.	(64-128)	48%	20%	79%	79%	39%	38%	19%	16%				
% Large cobbles.	(128-256)	0%	28%	10%	10%	14%	15%	15%	26%				
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	28%				

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 9/12/97	2, 9/12/97	3, 9/12/97	4, 9/12/97	1, 27/11/97	2, 27/11/97	3, 27/11/97	4, 27/11/97	1, 28/11/97	2, 28/11/97	3, 28/11/97	4, 28/11/97
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	689.57	276.77	267.22	253.76	813.79	627.58	329.05	992.65	194.36	103.80	359.63	343.16
Coarse gravel	32 mm - 16 mm	151.55	400.80	428.97	556.78	423.91	197.20	856.16	180.30	181.63	442.17	741.56	344.39
Medium gravel	16 mm - 8 mm	223.17	346.53	349.49	306.14	391.59	245.98	254.14	282.50	543.15	250.56	164.38	342.54
Fine gravel	8 mm - 4 mm	308.77	184.12	329.11	339.25	240.44	210.71	316.61	153.18	507.21	352.68	369.79	276.19
Very fine gravel	4 mm - 2 mm	147.92	149.23	109.10	128.10	75.59	48.53	179.06	85.18	201.19	314.57	184.96	123.50
Very coarse sand	2 mm - 1 mm	88.27	73.03	52.90	66.58	87.40	9.87	98.13	33.34	133.66	266.86	106.31	81.83
Coarse sand	1 mm - 0.5 mm	56.68	32.03	25.83	30.34	30.28	2.39	32.59	14.09	85.95	146.21	64.27	29.85
Medium sand	0.5 mm - 0.25 mm	61.28	33.43	27.90	29.04	16.61	1.55	19.80	14.86	140.82	94.17	64.06	15.66
Fine sand	0.25 mm - 0.125 mm	94.86	71.61	52.48	69.07	33.68	4.49	30.58	33.05	310.89	102.28	132.44	42.78
Very fine sand	0.125 mm - 0.063 mm	36.18	47.03	38.06	36.46	14.15	6.14	19.71	18.43	93.41	35.59	58.53	26.18
Silt	< 0.063 mm	5.84	13.48	10.79	11.53	1.15	0.63	2.38	4.23	12.83	7.47	14.16	9.09
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	2%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Small gravel.	(2-32)	14%	9%	27%	4%	18%	22%	3%	5%	5%	5%	5%	5%
% Large gravel.	(32-64)	14%	21%	9%	39%	52%	54%	65%	44%	10%	25%	10%	25%
% Small cobbles.	(64-128)	19%	55%	19%	17%	21%	24%	18%	42%	85%	70%	85%	70%
% Large cobbles.	(128-256)	26%	15%	44%	40%	8%	0%	13%	9%	0%	0%	0%	0%
% Boulders.	(256-332)	26%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
bed composition (g)													
	Size Class	Minor				Major							
		1, 27/11/97	2, 27/11/97	3, 27/11/97	4, 27/11/97	1, 27/11/97	2, 27/11/97	3, 27/11/97	4, 27/11/97				
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
Very coarse gravel	64 mm - 32 mm	391.76	160.85	171.30	592.92	825.39	514.38	439.00	186.49				
Coarse gravel	32 mm - 16 mm	140.50	804.55	386.70	255.76	181.23	283.89	302.15	183.88				
Medium gravel	16 mm - 8 mm	229.72	435.52	314.14	356.41	249.48	385.62	434.13	242.04				
Fine gravel	8 mm - 4 mm	277.53	346.81	262.70	196.56	34.01	202.91	352.77	212.72				
Very fine gravel	4 mm - 2 mm	136.74	223.72	82.44	112.72	20.95	110.42	206.79	131.38				
Very coarse sand	2 mm - 1 mm	64.17	146.11	30.90	65.58	14.68	71.49	110.57	85.03				
Coarse sand	1 mm - 0.5 mm	20.56	57.42	11.39	19.02	4.98	18.35	33.72	33.47				
Medium sand	0.5 mm - 0.25 mm	20.24	39.32	9.34	16.40	6.02	18.65	24.53	28.45				
Fine sand	0.25 mm - 0.125 mm	53.26	98.29	17.61	43.46	16.14	53.69	60.54	66.34				
Very fine sand	0.125 mm - 0.063 mm	31.67	90.35	25.00	39.95	17.96	41.01	60.87	66.28				
Silt	< 0.063 mm	3.83	13.17	3.47	7.03	3.07	5.09	12.92	8.79				
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%				
% Small gravel.	(2-32)	0%	3%	2%	3%	0%	0%	0%	0%				
% Large gravel.	(32-64)	75%	57%	46%	55%	70%	44%	75%	62%				
% Small cobbles.	(64-128)	17%	7%	8%	5%	6%	0%	25%	13%				
% Large cobbles.	(128-256)	9%	33%	12%	36%	24%	56%	0%	25%				
% Boulders.	(256-332)	0%	0%	32%	0%	0%	0%	0%	0%				

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 2/3/98	2, 2/3/98	3, 2/3/98	4, 2/3/98	1, 5/3/98	2, 5/3/98	3, 5/3/98	4, 5/3/98	1, 10/1/98	2, 10/1/98	3, 10/1/98	4, 10/1/98
Small cobble	128 mm - 64 mm	605.20	0.00	0.00	0.00	0.00	0.00	518.80	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	94.47	701.40	620.00	649.30	748.60	897.40	588.20	440.00	759.40	904.50	553.40	1154.15
Coarse gravel	32 mm - 16 mm	544.12	644.74	320.66	166.29	638.75	430.11	451.53	624.95	333.58	276.74	371.97	439.37
Medium gravel	16 mm - 8 mm	294.08	361.91	539.73	226.14	369.90	287.13	282.56	459.15	235.06	159.28	286.63	273.97
Fine gravel	8 mm - 4 mm	205.92	206.63	439.11	168.25	193.26	191.32	130.84	266.46	82.95	78.23	94.09	91.73
Very fine gravel	4 mm - 2 mm	141.79	146.03	180.73	150.46	111.85	143.12	78.30	161.70	35.09	24.80	4.78	46.35
Very coarse sand	2 mm - 1 mm	53.90	64.82	47.36	83.45	65.77	62.36	40.74	64.51	19.09	4.93	0.00	19.32
Coarse sand	1 mm - 0.5 mm	35.78	17.98	38.60	50.99	43.51	24.00	23.12	25.49	13.29	2.48	0.04	13.16
Medium sand	0.5 mm - 0.25 mm	107.72	40.52	140.28	61.79	54.14	26.41	35.38	35.51	18.90	4.03	0.00	34.42
Fine sand	0.25 mm - 0.125 mm	65.63	39.86	95.96	29.30	40.76	33.22	34.88	51.72	13.46	4.69	0.04	23.70
Very fine sand	0.125 mm - 0.063 mm	22.04	13.53	32.55	10.20	18.66	19.54	21.99	28.75	3.75	2.72	0.15	8.60
Silt	< 0.063 mm	19.19	11.39	23.04	15.77	18.25	18.40	21.76	28.79	2.85	4.06	1.49	9.43
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	3%	3%	0%	0%	0%	0%	0%	0%	0%	0%
% Small gravel.	(2-32)	8%	0%	9%	35%	11%	3%	16%	9%	2%	0%	3%	2%
% Large gravel.	(32-64)	43%	11%	17%	26%	43%	49%	24%	37%	19%	16%	29%	17%
% Small cobbles.	(64-128)	16%	9%	17%	23%	47%	35%	43%	54%	54%	45%	55%	26%
% Large cobbles.	(128-256)	34%	80%	23%	13%	0%	13%	16%	0%	25%	38%	13%	55%
% Boulders.	(256-332)	0%	0%	31%	0%	0%	0%	0%	0%	0%	0%	0%	0%
bed composition (g)													
	Size Class	Minor				Major							
		1, 2/3/98	2, 2/3/98	3, 2/3/98	4, 2/3/98	1, 5/3/98	2, 5/3/98	3, 5/3/98	4, 5/3/98				
Small cobble	128 mm - 64 mm	905.80	0.00	0.00	0.00	456.40	0.00	0.00	0.00				
Very coarse gravel	64 mm - 32 mm	0.00	520.00	422.70	869.10	690.00	383.36	918.60	602.30				
Coarse gravel	32 mm - 16 mm	116.68	272.93	452.80	259.72	377.50	377.14	286.20	436.12				
Medium gravel	16 mm - 8 mm	161.32	199.90	254.03	173.10	183.35	217.60	297.52	307.39				
Fine gravel	8 mm - 4 mm	56.92	103.74	126.24	103.08	134.71	147.91	187.30	195.53				
Very fine gravel	4 mm - 2 mm	16.08	62.30	81.53	71.84	85.06	111.76	137.92	164.73				
Very coarse sand	2 mm - 1 mm	3.57	31.78	32.60	33.48	43.73	62.07	64.95	98.50				
Coarse sand	1 mm - 0.5 mm	1.15	18.34	17.19	19.78	28.24	31.77	31.11	54.38				
Medium sand	0.5 mm - 0.25 mm	1.51	25.64	34.15	23.89	40.38	63.15	103.60	147.13				
Fine sand	0.25 mm - 0.125 mm	1.93	19.24	24.57	23.44	17.01	31.55	75.82	75.23				
Very fine sand	0.125 mm - 0.063 mm	0.54	3.81	7.57	5.17	3.48	5.64	16.57	13.57				
Silt	< 0.063 mm	1.51	2.82	2.67	5.58	3.48	5.16	9.07	5.72				
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%				
% Small gravel.	(2-32)	2%	26%	6%	3%	41%	32%	28%	3%				
% Large gravel.	(32-64)	38%	18%	84%	51%	3%	14%	7%	50%				
% Small cobbles.	(64-128)	24%	18%	0%	27%	17%	25%	10%	12%				
% Large cobbles.	(128-256)	36%	38%	10%	20%	39%	30%	11%	35%				
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	44%	0%				

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 18/4/98	2, 18/4/98	3, 18/4/98	4, 18/4/98	1, 21/4/98	2, 21/4/98	3, 21/4/98	4, 21/4/98	1, 23/4/98	2, 23/4/98	3, 23/4/98	4, 23/4/98
Small cobble	128 mm - 64 mm	0.00	0.00	411.30	0.00	0.00	0.00	779.20	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	880.50	574.60	580.70	737.89	435.10	312.30	379.03	727.80	556.60	749.90	0.00	300.11
Coarse gravel	32 mm - 16 mm	423.98	438.47	267.52	369.03	265.64	147.59	217.43	237.00	367.28	438.65	226.27	641.35
Medium gravel	16 mm - 8 mm	212.55	390.22	313.39	373.56	304.97	431.64	249.46	286.11	524.52	689.75	334.03	426.05
Fine gravel	8 mm - 4 mm	86.31	309.05	167.94	189.56	196.03	295.15	161.02	323.80	252.83	362.54	108.95	230.72
Very fine gravel	4 mm - 2 mm	41.26	231.61	96.56	146.08	121.73	234.11	79.75	237.48	142.81	163.67	64.88	141.11
Very coarse sand	2 mm - 1 mm	40.08	93.92	48.19	84.64	69.31	136.32	40.07	116.29	82.88	91.73	51.47	91.82
Coarse sand	1 mm - 0.5 mm	72.00	72.48	43.12	75.03	52.69	81.29	27.97	66.00	69.60	99.70	46.74	83.13
Medium sand	0.5 mm - 0.25 mm	102.00	165.54	77.99	132.81	76.83	126.60	65.57	130.15	142.85	144.16	73.66	142.73
Fine sand	0.25 mm - 0.125 mm	142.86	61.71	35.38	49.78	34.83	74.04	54.86	68.61	80.21	57.33	39.94	73.64
Very fine sand	0.125 mm - 0.063 mm	45.84	12.69	9.74	14.21	11.90	18.89	20.83	15.16	17.86	12.82	12.45	18.70
Silt	< 0.063 mm	9.05	13.01	6.93	10.20	9.86	10.78	10.66	10.69	17.39	8.60	8.48	13.70
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	0%	0%	0%	0%	1%	27%	0%	0%	0%	0%
% Small gravel.	(2-32)	17%	10%	40%	71%	2%	14%	9%	27%	19%	23%	31%	24%
% Large gravel.	(32-64)	44%	39%	7%	8%	7%	5%	10%	0%	11%	6%	4%	11%
% Small cobbles.	(64-128)	40%	15%	54%	8%	59%	21%	32%	24%	63%	62%	46%	38%
% Large cobbles.	(128-256)	0%	36%	0%	13%	33%	60%	49%	21%	7%	9%	18%	27%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
bed composition (g)													
	Size Class	Minor				Major							
		1, 21/4/98	2, 21/4/98	3, 21/4/98	4, 21/4/98	1, 23/4/98	2, 23/4/98	3, 23/4/98	4, 23/4/98				
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	0.00	467.00	0.00	0.00				
Very coarse gravel	64 mm - 32 mm	510.10	911.70	760.40	933.60	905.80	415.80	784.38	903.00				
Coarse gravel	32 mm - 16 mm	690.67	521.77	445.50	226.32	498.50	402.39	513.76	465.31				
Medium gravel	16 mm - 8 mm	412.49	341.38	285.68	404.47	556.16	280.15	245.35	278.54				
Fine gravel	8 mm - 4 mm	208.81	128.08	107.59	195.67	351.19	172.82	24.59	113.59				
Very fine gravel	4 mm - 2 mm	123.60	81.36	63.92	92.42	56.01	70.11	0.66	7.80				
Very coarse sand	2 mm - 1 mm	59.86	34.05	25.89	29.88	14.16	19.68	0.00	0.21				
Coarse sand	1 mm - 0.5 mm	34.91	23.04	17.27	17.92	11.97	11.67	0.00	0.00				
Medium sand	0.5 mm - 0.25 mm	63.83	76.92	67.11	33.74	77.20	42.18	0.00	0.00				
Fine sand	0.25 mm - 0.125 mm	62.08	86.72	79.45	26.85	72.04	57.19	0.00	0.00				
Very fine sand	0.125 mm - 0.063 mm	14.17	19.38	19.62	13.29	12.53	21.34	0.00	0.00				
Silt	< 0.063 mm	5.26	5.71	8.11	13.19	4.80	6.25	0.00	0.00				
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	4%	0%				
% Small gravel.	(2-32)	0%	2%	0%	0%	54%	30%	64%	25%				
% Large gravel.	(32-64)	43%	38%	28%	52%	25%	44%	11%	23%				
% Small cobbles.	(64-128)	41%	31%	14%	28%	21%	26%	22%	20%				
% Large cobbles.	(128-256)	17%	29%	17%	20%	0%	0%	0%	32%				
% Boulders.	(256-332)	0%	0%	42%	0%	0%	0%	0%	0%				

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 18/5/98	2, 18/5/98	3, 18/5/98	4, 18/5/98	1, 25/5/98	2, 25/5/98	3, 25/5/98	4, 25/5/98	1, 21/5/98	2, 21/5/98	3, 21/5/98	4, 21/5/98
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	711.29	682.83	608.40	187.40	390.10	713.94	660.40	319.70	868.15	746.80	116.50	894.50
Coarse gravel	32 mm - 16 mm	521.78	281.38	489.20	249.61	490.58	539.69	524.03	581.63	431.33	419.29	887.44	473.73
Medium gravel	16 mm - 8 mm	375.18	279.53	338.77	371.13	318.71	192.27	637.91	491.29	116.31	416.41	505.66	220.60
Fine gravel	8 mm - 4 mm	168.55	119.52	184.66	272.35	168.14	55.70	154.61	254.25	26.90	165.14	339.96	57.43
Very fine gravel	4 mm - 2 mm	95.90	94.04	103.58	177.01	111.17	30.10	22.06	143.41	8.71	48.31	19.78	34.25
Very coarse sand	2 mm - 1 mm	53.05	58.50	42.31	87.29	65.59	18.82	4.46	101.23	7.93	13.92	12.32	21.24
Coarse sand	1 mm - 0.5 mm	48.33	44.38	22.05	56.95	48.83	16.44	1.86	102.00	13.42	21.42	22.08	22.06
Medium sand	0.5 mm - 0.25 mm	98.24	56.68	43.53	111.37	69.83	26.03	2.34	123.71	53.33	63.45	64.91	67.87
Fine sand	0.25 mm - 0.125 mm	50.28	18.99	38.37	51.66	21.62	13.52	1.32	24.82	57.83	70.70	67.89	76.72
Very fine sand	0.125 mm - 0.063 mm	17.94	4.08	13.17	10.46	4.57	4.36	0.54	15.59	16.47	17.53	16.37	23.49
Silt	< 0.063 mm	14.48	4.65	12.47	8.76	10.34	24.03	2.00	15.48	8.64	9.56	7.75	8.83
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	2%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Small gravel.	(2-32)	32%	34%	29%	45%	54%	54%	50%	48%	61%	52%	64%	60%
% Large gravel.	(32-64)	4%	11%	14%	7%	24%	14%	23%	23%	11%	23%	8%	14%
% Small cobbles.	(64-128)	35%	37%	17%	5%	23%	32%	27%	28%	29%	25%	8%	27%
% Large cobbles.	(128-256)	29%	17%	37%	43%	0%	0%	0%	0%	0%	0%	20%	0%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

bed composition (g)		Minor				Major			
	Size Class	1, 25/5/98	2, 25/5/98	3, 25/5/98	4, 25/5/98	1, 21/5/98	2, 21/5/98	3, 21/5/98	4, 21/5/98
Small cobble	128 mm - 64 mm	0.00	0.00	473.20	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	750.50	777.10	232.20	428.50	1095.79	767.40	450.00	657.40
Coarse gravel	32 mm - 16 mm	574.21	505.84	339.56	504.68	288.81	380.02	622.23	600.61
Medium gravel	16 mm - 8 mm	447.83	372.22	296.60	283.83	244.54	531.07	383.71	283.14
Fine gravel	8 mm - 4 mm	130.97	161.89	176.53	262.13	52.83	219.38	213.43	213.35
Very fine gravel	4 mm - 2 mm	53.94	90.88	77.03	141.13	7.59	39.75	56.81	65.90
Very coarse sand	2 mm - 1 mm	26.30	36.63	29.45	67.32	0.88	1.35	12.47	28.73
Coarse sand	1 mm - 0.5 mm	26.07	25.03	21.17	46.87	0.35	0.16	6.58	24.58
Medium sand	0.5 mm - 0.25 mm	84.86	69.79	55.59	100.29	0.93	0.50	15.48	79.18
Fine sand	0.25 mm - 0.125 mm	73.79	49.74	44.39	73.88	0.75	0.76	10.21	48.52
Very fine sand	0.125 mm - 0.063 mm	18.49	12.15	10.73	16.27	0.23	0.16	1.53	10.01
Silt	< 0.063 mm	7.22	7.77	4.38	7.53	0.06	0.02	1.73	5.22
Visual assessment of surface composition									
% Silt.		0%	0%	11%	4%	0%	0%	0%	0%
% Sand.	<2	0%	0%	0%	4%	0%	0%	0%	0%
% Small gravel.	(2-32)	48%	26%	29%	16%	59%	41%	54%	61%
% Large gravel.	(32-64)	17%	63%	39%	61%	11%	2%	26%	14%
% Small cobbles.	(64-128)	13%	11%	21%	15%	30%	49%	20%	25%
% Large cobbles.	(128-256)	23%	0%	0%	0%	0%	8%	0%	0%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%



bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 30/6/98	2, 30/6/98	3, 30/6/98	4, 30/6/98	1, 30/6/98	2, 30/6/98	3, 30/6/98	4, 30/6/98	1, 5/7/98	2, 5/7/98	3, 5/7/98	4, 5/7/98
Small cobble	128 mm - 64 mm	0.00	0.00	412.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	563.66	123.67	547.80	584.00	677.70	816.50	132.40	623.78	550.00	175.65	808.80	275.70
Coarse gravel	32 mm - 16 mm	635.20	692.38	515.50	377.73	586.68	437.41	363.21	617.20	443.36	234.40	393.27	220.20
Medium gravel	16 mm - 8 mm	318.16	496.72	233.48	308.14	431.28	485.29	479.68	267.54	417.91	219.72	266.39	250.72
Fine gravel	8 mm - 4 mm	166.69	250.20	133.62	160.65	163.81	181.96	253.76	233.71	311.39	126.42	196.82	206.23
Very fine gravel	4 mm - 2 mm	103.11	144.89	99.73	107.38	74.60	79.43	111.42	131.69	180.64	69.75	158.27	164.38
Very coarse sand	2 mm - 1 mm	88.75	96.02	83.96	89.47	41.70	34.91	39.80	41.83	74.32	28.66	86.23	89.56
Coarse sand	1 mm - 0.5 mm	86.43	110.55	103.75	120.53	51.63	54.35	20.69	25.70	33.78	13.14	52.35	44.88
Medium sand	0.5 mm - 0.25 mm	70.06	104.23	76.69	286.17	110.40	128.60	49.07	69.87	91.47	26.64	100.07	84.02
Fine sand	0.25 mm - 0.125 mm	16.35	24.76	15.04	83.69	17.53	22.82	19.35	37.80	105.03	30.96	83.89	69.73
Very fine sand	0.125 mm - 0.063 mm	7.52	7.01	4.64	9.66	2.48	10.14	9.56	12.24	34.38	8.62	21.30	19.08
Silt	< 0.063 mm	13.69	13.35	8.05	8.64	6.01	15.56	23.44	13.71	18.92	7.94	12.05	19.63
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2%	0%
% Small gravel.	(2-32)	35%	54%	51%	64%	26%	41%	48%	28%	24%	41%	42%	16%
% Large gravel.	(32-64)	42%	15%	10%	10%	20%	16%	2%	5%	20%	21%	8%	8%
% Small cobbles.	(64-128)	23%	31%	15%	26%	28%	43%	33%	60%	31%	14%	22%	21%
% Large cobbles.	(128-256)	0%	0%	24%	0%	26%	0%	17%	7%	25%	24%	25%	10%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	45%
bed composition (g)													
	Size Class	Minor				Major							
		1, 5/7/98	2, 5/7/98	3, 5/7/98	4, 5/7/98	1, 5/7/98	2, 5/7/98	3, 5/7/98	4, 5/7/98				
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
Very coarse gravel	64 mm - 32 mm	575.56	681.20	689.00	325.67	424.62	654.60	1142.70	1051.30				
Coarse gravel	32 mm - 16 mm	710.81	414.50	220.36	658.36	772.63	472.67	592.81	298.35				
Medium gravel	16 mm - 8 mm	270.10	170.48	457.77	443.98	222.74	459.11	230.28	37.53				
Fine gravel	8 mm - 4 mm	85.24	56.01	337.92	131.34	6.83	79.92	45.65	0.00				
Very fine gravel	4 mm - 2 mm	52.06	15.23	188.49	63.12	0.00	3.27	7.20	0.00				
Very coarse sand	2 mm - 1 mm	42.95	3.02	108.07	23.12	0.02	0.07	0.82	0.02				
Coarse sand	1 mm - 0.5 mm	55.25	1.44	145.08	22.65	0.34	0.04	0.83	0.04				
Medium sand	0.5 mm - 0.25 mm	45.43	1.59	170.41	55.36	0.00	0.07	6.76	0.06				
Fine sand	0.25 mm - 0.125 mm	17.13	2.91	45.34	30.84	0.00	0.08	12.85	0.22				
Very fine sand	0.125 mm - 0.063 mm	3.98	1.56	8.22	5.99	0.00	0.03	4.49	0.54				
Silt	< 0.063 mm	0.56	0.57	0.82	0.50	0.03	0.04	3.63	1.76				
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%				
% Small gravel.	(2-32)	35%	21%	61%	50%	57%	50%	72%	67%				
% Large gravel.	(32-64)	24%	20%	28%	21%	14%	22%	23%	17%				
% Small cobbles.	(64-128)	33%	45%	11%	29%	28%	28%	5%	16%				
% Large cobbles.	(128-256)	9%	13%	0%	0%	0%	0%	0%	0%				
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%				

bed composition (g)		Perennial seepage stream				Baseflow seepage stream				Baseflow spring stream			
	Size Class	1, 8/8/98	2, 8/8/98	3, 8/8/98	4, 8/8/98	1, 8/8/98	2, 8/8/98	3, 8/8/98	4, 8/8/98	1, 15/8/98	2, 15/8/98	3, 15/8/98	4, 15/8/98
Small cobble	128 mm - 64 mm	0.00	762.60	960.00	0.00	648.40	0.00	0.00	337.60	0.00	0.00	0.00	0.00
Very coarse gravel	64 mm - 32 mm	931.70	530.10	157.24	901.00	263.34	1084.70	578.60	660.00	347.22	796.10	331.66	422.60
Coarse gravel	32 mm - 16 mm	533.87	212.37	348.25	522.56	306.44	244.47	591.82	321.80	434.55	749.74	1032.79	1047.99
Medium gravel	16 mm - 8 mm	315.16	301.73	177.66	326.20	341.13	238.34	358.32	398.37	371.71	322.21	286.50	303.57
Fine gravel	8 mm - 4 mm	171.89	290.21	173.22	184.79	257.86	202.56	307.54	254.18	64.46	43.26	86.13	112.99
Very fine gravel	4 mm - 2 mm	84.56	172.22	121.90	93.29	252.66	171.26	193.23	158.39	13.93	0.97	21.22	27.89
Very coarse sand	2 mm - 1 mm	22.23	60.72	54.17	40.60	141.40	117.43	91.91	66.57	9.77	0.17	13.72	16.46
Coarse sand	1 mm - 0.5 mm	7.30	31.07	30.68	30.35	28.04	65.23	47.45	37.84	8.41	0.55	18.75	18.79
Medium sand	0.5 mm - 0.25 mm	25.86	94.02	82.92	99.85	43.76	117.63	93.27	120.00	17.04	1.94	38.74	22.47
Fine sand	0.25 mm - 0.125 mm	22.23	82.76	54.87	76.13	27.65	108.07	88.25	908.00	13.29	2.58	20.45	9.79
Very fine sand	0.125 mm - 0.063 mm	9.84	34.70	22.86	26.29	6.09	37.71	25.28	121.77	2.27	1.06	4.68	2.23
Silt	< 0.063 mm	0.50	1.57	0.80	1.83	0.20	0.88	1.05	0.69	0.49	1.17	2.36	1.10
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
% Sand.	<2	1%	0%	11%	0%	0%	0%	1%	0%	0%	0%	0%	0%
% Small gravel.	(2-32)	32%	9%	26%	8%	14%	41%	21%	13%	58%	85%	69%	61%
% Large gravel.	(32-64)	14%	11%	12%	0%	0%	15%	7%	3%	24%	15%	23%	36%
% Small cobbles.	(64-128)	14%	47%	9%	45%	19%	45%	30%	5%	18%	0%	8%	4%
% Large cobbles.	(128-256)	40%	33%	42%	47%	67%	0%	41%	30%	0%	0%	0%	0%
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	49%	0%	0%	0%	0%
bed composition (g)													
	Size Class	Minor				Major							
		1, 16/8/98	2, 16/8/98	3, 16/8/98	4, 16/8/98	1, 16/8/98	2, 16/8/98	3, 16/8/98	4, 16/8/98				
Small cobble	128 mm - 64 mm	0.00	0.00	0.00	0.00	448.50	0.00	259.96	0.00				
Very coarse gravel	64 mm - 32 mm	671.90	934.70	371.70	690.10	654.58	456.30	760.10	1034.60				
Coarse gravel	32 mm - 16 mm	511.85	460.25	506.44	566.84	96.30	525.84	182.65	270.95				
Medium gravel	16 mm - 8 mm	416.00	283.77	229.15	418.38	273.37	490.70	232.35	220.50				
Fine gravel	8 mm - 4 mm	153.87	129.85	113.53	153.83	224.92	251.83	243.51	125.39				
Very fine gravel	4 mm - 2 mm	110.09	73.51	78.04	54.92	190.12	231.23	214.10	91.88				
Very coarse sand	2 mm - 1 mm	72.41	41.24	47.60	26.00	126.72	161.67	139.98	63.57				
Coarse sand	1 mm - 0.5 mm	62.98	28.54	54.79	25.44	63.42	89.47	69.35	31.09				
Medium sand	0.5 mm - 0.25 mm	132.19	53.27	304.13	54.08	124.56	130.13	93.20	47.85				
Fine sand	0.25 mm - 0.125 mm	106.48	41.60	240.28	31.02	66.65	44.70	37.16	21.14				
Very fine sand	0.125 mm - 0.063 mm	20.68	11.59	57.48	6.33	13.30	11.26	11.03	5.89				
Silt	< 0.063 mm	0.67	0.39	1.89	0.94	8.14	7.84	9.93	6.26				
Visual assessment of surface composition													
% Silt.		0%	0%	0%	0%	0%	0%	0%	0%				
% Sand.	<2	0%	0%	0%	0%	0%	0%	0%	0%				
% Small gravel.	(2-32)	14%	14%	43%	4%	5%	4%	2%	2%				
% Large gravel.	(32-64)	63%	55%	11%	68%	10%	33%	32%	44%				
% Small cobbles.	(64-128)	16%	32%	47%	27%	85%	37%	67%	29%				
% Large cobbles.	(128-256)	8%	0%	0%	0%	0%	26%	0%	25%				
% Boulders.	(256-332)	0%	0%	0%	0%	0%	0%	0%	0%				